Disentangling the effects of disturbance and habitat size on stream community structure

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A thesis submitted for the Degree of

Doctor of Philosophy in Ecology

at the

University of Canterbury

by

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University of Canterbury

Christchurch, New Zealand

2011

In loving memory of my friend

Matthew Langley

1983 – 2009

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Abstract

Our ability to predict community responses to environmental stress remains limited. To address this issue, I investigated how species abundance, community composition and food-web structure varied across abiotic gradients (principally disturbance and habitat size) in New Zealand streams. In surveys, community composition, biomass and richness were all strongly influenced by flood-related habitat disturbance, although disturbance influenced each trophic level via different mechanisms. Experiments indicated that macroinvertebrate prey communities were primarily structured by physical disturbance effects, whereas predatory fish communities were structured by physical disturbance effects and disturbance-mediated changes to prey communities. Prey community biomass and composition affected fish species identity and abundance and an *in situ* stream channel experiment suggested that prey communities were structured by trade-offs between resisting biotic interactions in physically stable environments and successfully exploiting highly disturbed habitats. The prey community traits associated with different disturbance regimes then directly influenced the composition and predatory impact of the resultant fish communities. In addition to disturbance-mediated biotic interactions, abiotic gradients also provided strong selection pressures on predatory fish communities. In particular, disturbance and habitat size strongly influenced predator community responses (e.g., biomass and maximum body size) in surveys and experiments. However, a habitat's capacity to support predator community biomass was largely determined by its size. Food-web structure changed with habitat size; small streams supported more prey than predator biomass, whereas large streams had inverted biomass pyramids (i.e., more predator than prey biomass). Similar relationships between food-web structure and habitat size were found in grassland and forested streams, but terrestrial invertebrate subsidies meant that forested streams supported more predator biomass per unit area than grassland stream food webs. My results indicate that human actions resulting in habitat loss (e.g., water abstraction or river impoundment) and increases in flood-related disturbance events (e.g., climate change) are likely to have significant impacts on stream food webs, ultimately leading to habitats that support smaller fish communities (i.e., less biomass, smaller body size). This means that ecologists and managers will need to consider the separate, interactive and indirect effects of disturbance and habitat size on ecological communities if we are to accurately predict and manage food-web responses to global environmental change.

Frontispiece. A view of the alpine headwaters of the upper Waimakariri River (Photo credit: Angus McIntosh).

Chapter One

General Introduction

Globally, ecosystems are experiencing unprecedented levels of pressure due to pervasive impacts from land-use intensification, habitat fragmentation, species invasions, over exploitation and climate warming (Vitousek et al. 1997, IPCC 2001, Foley et al. 2005, Banavar & Maritan 2009). Consequently, one of the main challenges confronting ecologists is to understand and predict how the composition of biological communities may vary given rapid global change (Agrawal et al. 2007). Global change drivers are already having significant impacts on ecosystems (Didham et al. 2007, Tylianakis et al. 2008), and some of the strongest effects are being observed in freshwater environments (e.g., freshwater biodiversity is declining at greater rates than even the most affected terrestrial ecosystems, Ricciardi & Rasmussen 1999). In particular, riverine ecosystems have been subjected to extensive anthropogenic alteration for water, energy, transportation and recreational needs (Nilsson et al. 2005). Whilst it is widely recognised that these actions have significant impacts on biodiversity, understanding of the ecological consequences is limited (Banavar & Maritan 2009). Our inability to predict such consequences arises from significant "gaps" in our current knowledge of community ecology. In reviewing ecological knowledge, Agrawal et al. (2007) identified understanding how abiotic and biotic contexts shape species distribution, abundance and interaction strength over space or time as the major limitation to advances in general ecological theory. To address this knowledge gap, I investigated how species abundance, community composition and food-web structure varied across abiotic gradients (principally disturbance and habitat size) and under different biotic contexts in New Zealand streams.

Disturbance and its influence on stream food webs

Disturbance is one of the major abiotic factors determining community composition because it alters the relative importance of biotic and abiotic processes (e.g., Peckarsky 1983, Menge & Sutherland 1987). Biotic interactions (e.g., predation, competition) are predicted to strongly influence communities in low disturbance (i.e., benign) conditions, but as disturbance increases, the relative importance of biotic interactions is predicted to weaken as physical processes increasingly determine community structure (Menge & Sutherland 1987). Moreover, across gradients of disturbance, species vary in the traits they possess, because there is a trade-off between traits for resistance/resilience to disturbance (e.g., high mobility, fast growth rates) and those that confer resistance to biotic interactions under more benign conditions (e.g., morphological defences) (Werner & Anholt 1993, Power et al. 1996, Wellborn et al. 1996, Grime 2001). This can result in changes to community structure along the disturbance gradient because species with reduced vulnerability to predation or competition are usually more susceptible to disturbance (Wellborn et al. 1996, Wootton et al. 1996, Greig & Wissinger 2010). Thus, strong biotic interactions may occur in stable habitats (Power et al. 1996, Wootton et al. 1996), but highly disturbed conditions may ameliorate strong biotic interactions and populations may be composed of species which may otherwise be out-competed or eliminated by predators under more stable conditions (Allan & Castillo 2007).

In addition to biotic interactions and abiotic factors, disturbance can influence a range of other ecological processes (e.g., dispersal, resource acquisition), so disturbance is now considered a fundamental driver in stream ecology (Resh et al. 1988, Power 1992a, Wootton et al. 1996, Death 2008, Stanley et al. 2010). For a disturbance event to have occurred, organisms must be affected (Poff 1992), so disturbance is generally defined by its ecological effects. In stream ecology there are three distinct types of disturbance and they vary based on

the temporal strength of the disturbing force(s) (see Lake 2000). Globally, floods (classified as a pulse disturbance) are likely to be the most common type of stream disturbance event, and although flood attributes may vary between systems, they are generally associated with increased water velocity that causes sediment, rock and debris to be mobilised within the stream channel. Flow-related disturbance effects on ecological processes vary with the magnitude, frequency, duration, timing and rate of change of the flood event (Poff et al. 1997), although the effects on species and communities are via direct or indirect effects (Hart & Finelli 1999). Direct disturbance effects largely occur due to hydrodynamic forces affecting the "performance" of an organism (i.e., injury or death), whereas indirect effects influence organisms via a change in another factor/variable, for example, a reduction in resource supply (Nyström et al. 2003) or a change in predator-prey interaction strength (Wootton et al. 1996, Townsend et al. 1998). Whilst disturbance can have a range of effects on stream communities, it is still not clear how abiotic and biotic factors interact in stream ecosystems or how abiotic and biotic contexts influence species interactions (Agrawal et al. 2007). Thus, I will evaluate how disturbance can alter stream community structure by assessing how the relative importance of abiotic and biotic processes varies using surveys, mesocosm experiments and *in situ* manipulations.

Habitat size – a new take on an old concept

One of the most important characteristics of a habitat or ecosystem is its size (Levin 1992, Polis & Strong 1996). Habitat size (also termed ecosystem size) has long been known to influence ecological communities through effects on body size (McNab 1963, Harestad & Bunnel 1979) and species richness (e.g., island biogeography theory, MacArthur & Wilson 1967), and although these relationships were originally established in terrestrial ecosystems, positive relationships between habitat size and both body size and species richness have been

observed in freshwater environments (Minns 1995, Griffiths 1997, Poff et al. 2001). Moreover, recent modelling suggests habitat size could be particularly important for structuring food webs (e.g., McCann et al. 2005). Empirical research investigating the relationship between habitat size and food-chain length has shown the importance of size, because larger ecosystems support longer food-chains (Spencer & Warren 1996, Vander Zanden et al. 1999, Post et al. 2000, Thompson & Townsend 2005, McHugh et al. 2010). Food-chain length is also an important characteristic of ecological communities because it alters trophic interactions and community structure (Post 2002). Thus, habitat size is an important determinant of food-web structure. Moreover, alterations in habitat size have been linked to changes in colonisation and extinction processes, species diversity and other food-web attributes such as interaction strength, body size and stability (MacArthur & Wilson 1967, Polis & Strong 1996, Spencer & Warren 1996, Vander Zanden et al. 1999, Post 2002, McCann et al. 2005). Within stream ecosystems, I expect that all these food-web attributes are likely to play a role in determining food-web structure, although their importance may vary with changes in the strength of abiotic factors. Prior to commencing my Ph. D research, we (Angus McIntosh and I) had found that habitat size was linked to changes in food-web structure in Canterbury streams. One of the major objectives of my thesis was to determine how variation in habitat size may influence a range of food-web attributes, and also how these attributes may combine to influence food-web structure.

Landscape-scale thinking in stream ecology

The ecology of streams is increasingly being considered in a landscape context, with food webs seen as the result of broader ecological processes and complex species interactions operating over larger scales than have typically been studied in the past (i.e., reach scale or smaller) (Wiens 2002). This "riverscape" research is needed to build a comprehensive

understanding of how communities may be structured and at what scale influential processes operate (Fausch et al. 2002). Such a framework allows stream ecologists to integrate concepts likely to influence food webs, such as metapopulation dynamics, landscape connectivity and spatial variation in habitat quality, into their research (Polis et al. 1997). However, to underpin such a framework, knowledge is required regarding how variation in abiotic factors will influence stream communities because abiotic factors may vary spatially and/or temporally within a catchment. For example, because streams form hierarchical spatial networks, habitat size will generally increase with distance downstream (although flow reductions due to drought or porous river material are notable exceptions), but size is likely to be highly temporally variable due to unpredictable flood-related events altering habitat size.

Linking relationships between large-scale spatial and temporal variation with critical biological processes, such as changes in the abundance of invertebrate and fish communities, should lead to insights into the role spatial scale plays in controlling the population and community dynamics of stream organisms (Schlosser 1991). Such studies should also enhance our ability to predict what impact spatial and temporal landscape-scale changes will have on stream communities because climate change is expected to change habitat size and alter disturbance regimes (IPCC 2001, Milly et al. 2005). Research investigating large-scale drivers is urgently needed, because the impact to river flow alterations of climate change effects is expected to surpass those currently caused by impoundments and abstraction by 2050 (Döll & Zhang 2010). Fresh water is widely regarded as the most essential natural resource, and striking a balance between human water use/security and biodiversity is going to be a difficult challenge, requiring sound science to guide decision-making processes at both a local and global scale (Vörösmarty et al. 2010). Thus, in this thesis research I focussed on investigating large-scale drivers of riverine food-web structure by assessing how alterations to

river flow (e.g., through shifts in habitat size or changes to disturbance regimes) could affect the structuring of stream communities.

Thesis organisation

I have structured my thesis as a series of stand alone scientific papers that will be submitted for publication. This format means that some repetition in the methods sections of chapters may be apparent, but I consider this to be the most effective way of presenting my research. In Chapter Two, I assessed a range of stream disturbance measures to determine the most appropriate measure for fish populations. I also used intensive surveys (temporal sampling of 20 sites) and extensive surveys (spatial sampling of 52 sites) to evaluate how disturbance is likely to influence stream biota. In particular, I tested whether stream communities, especially fish, were directly influenced by flow and if biotic interactions played a role in structuring communities.

In Chapter Three, I used a combination of surveys and experiments to test whether disturbance-mediated prey assemblages determined fish community structure. Changes in invertebrate and fish community composition were initially assessed across a disturbance gradient using stream surveys. To evaluate whether invertebrate community composition could affect fish communities, predation rates of different fish species (on contrasting prey assemblages) were measured in a mesocosm experiment. Furthermore, to assess whether different prey assemblages influenced fish community structure, an *in situ* experiment was conducted measuring the response of fishes to disturbance-mediated changes in prey communities.

Disturbance can strongly influence stream food webs, but other large-scale drivers such as habitat size and temperature should also be important. The effect of all three drivers on top predator body size was evaluated in Chapter Four because top predators are likely to be

disproportionately important in structuring ecological communities (McCann et al. 2005). I used field surveys to determine how these three drivers interacted to affect top predator body size, then conducted field experiments with contrasting habitat size and disturbance effects to tease apart how reductions in habitat size and increases in disturbance influenced top predator body size.

Previous research (conducted by Angus McIntosh and I) had found that food webs in grassland streams become increasingly inverted as habitat size increased (i.e., an increasing amount of predator biomass was supported by the same amount of prey biomass as streams became larger). In Chapter 5, I examined the drivers of this change in food-web structure and also whether a similar change in structure occurred in contrasting stream systems (e.g., grassland vs. forested streams). Forested streams often have a different resource base than grassland streams (e.g., detritus vs. algae) resulting in different assemblages, and these forested stream food webs can also be strongly influenced by the addition of terrestrial invertebrates (Nakano & Murakami 2001). I surveyed forested streams across a habitat-size gradient (and additional grassland sites) to investigate whether the previously observed relationship between food-web structure and habitat size would be present in these forested streams that were likely to be influenced by terrestrial subsidies.

In the final chapter (Chapter 6), I integrate the results and conclusions from this research and outline how it improves understanding of stream communities. I highlight the most important drivers of stream community structure and examine how these studies contribute to advancing ecological theory. Finally, I discuss how this research could provide a framework for ecosystem management in stream systems.

Each data chapter is multi-authored, but the analysis and writing are largely my own. Figures and tables are numbered from the beginning within each chapter, while all references are provided at the end of the thesis to avoid repetition. Most of the chapters have appendices

included because I intend to include these data as supplementary material when the chapters are published. Throughout this thesis, there is a paper referenced as Jellyman & McIntosh (2010). Prior to and during my thesis, experiments, analysis and writing were conducted for this paper. However, much of the original survey data was collected as part of a Bachelor of Science (Honours) project, so it is not included as a thesis chapter.

Plate 1. Gravel-bed rivers, typical of the Canterbury high-country, are often harsh habitats for stream biota to live in.

Chapter Two

Is disturbance a main driver of variability in stream fish communities?

Abstract

Flood-related disturbance events can strongly influence stream communities and being able to predict how community structure will respond both spatially and temporally to changes in disturbance regimes, is an important goal in stream ecology. To achieve this, researchers require disturbance measures that correlate well with community variability. A range of measures have been tested for stream periphyton and invertebrate communities, but studies assessing variation in fish assemblages have largely focussed on flow measures with other disturbance measures rarely being tested. I assessed various disturbance measures (e.g., flow, bed movement, bed classification index) by sampling twenty streams on multiple occasions to investigate whether fish communities were directly influenced by flow variability or if flow effects on bed movement were better related to fish community responses to flood disturbance. A separate one-off survey of 52 streams was used to assess whether disturbance directly affected fishes or whether disturbance determined fish communities via its effect on food supply (i.e., invertebrates). Bed-movement measures were generally very good predictors of fish communities as results from sampling twenty streams over time showed bed-movement was a strong determinant of both spatial and temporal variability in fish biomass and community structure. As streams became more disturbed, community biomass and structure became increasingly variable. A path analysis using the one-off stream survey showed that both physical habitat and food supply had equivalent effects on fish biomass, indicating that disturbance could influence fish biomass through both direct (i.e., physical) and indirect (i.e., food) pathways. Disturbance events that occur due to flooding can have a

wide range of impacts on stream ecosystems, so it is probably naïve to assume that flow alone will accurately predict changes to fish communities. My results suggest that variation in fish communities can be best understood by measuring flow-related bed movement, because bed disturbance is likely to better encompass major factors that influence stream fishes such as habitat availability and food supply.

Introduction

Humans are having an unprecedented impact on earth's climate (IPCC 2001) resulting in accelerated rates of population and species extinction (Vitousek et al. 1997, Duffy 2003). However, we currently lack the ability to predict the effect of climate change on communities because our understanding of how environmental changes influence spatial and temporal variation in communities is poor. Moreover, a strong focus on environmental factors that affect communities across different ecosystems is required so that research findings are widely applicable and not system-specific (Agrawal et al. 2007). Natural disturbance is a strong community structuring force in many ecosystems (e.g., terrestrial, marine, freshwater; Sousa 1984, Pickett & White 1985, Parker & Huryn 2006, Lepori & Malmqvist 2009), however, natural disturbance regimes are predicted to be seriously altered by climate change mechanisms such as reduced precipitation and temperature-induced increases in evapotranspiration (IPCC 2001, Xenopoulos & Lodge 2006). To forecast and possibly mitigate climate change effects, a greater understanding of the influence of disturbance on communities is required. Climate warming is predicted to disproportionately impact higher trophic levels (Petchey et al. 1999, Strecker et al. 2004, Daufresne et al. 2009) because larger organisms are more vulnerable to extinction than small organisms due to traits such as long life histories and high energetic demands. I investigated how stream fish communities (i.e.,

the top trophic level in these ecosystems) varied across a gradient of natural flood-related disturbance to enhance understanding of the effects of disturbance on higher trophic levels.

Disturbance gradients are strong determinants of communities because they affect species abundance, biomass, and diversity (Connell 1978, Fisher et al. 1982, Pickett & White 1985, Death & Winterbourn 1994, 1995, Townsend et al. 1997a, Lake 2000). Some theory suggests that in benign, predictable environments, biotic interactions are likely to be important in structuring communities, but as environments become more disturbed, communities will be increasingly influenced by stochastic processes (Menge & Sutherland 1987, Ives et al. 2003). Effectively, community structure is expected to be less predictable as environments become increasingly disturbed (Fisher et al. 1982, Death & Winterbourn 1994, but see Lepori & Malmqvist 2007 for an exception). These ideas have been tested using mainly periphyton and invertebrate communities in stream ecosystems (e.g., Death & Winterbourn 1994, 1995, Clausen & Biggs 1997, Townsend et al. 1997b), where species traits and richness often vary with disturbance resulting in changes to the biomass and structure of communities. However, much less is known about how stream fish communities respond to changes in disturbance, although reductions in biomass and changes in community structure might be expected as disturbance increases, because disturbance is likely to have important impacts on the habitat availability and food supply of fishes (Meffe & Minckley 1987, Sircom & Walde 2009).

The uncertainty surrounding the effects of disturbance on fish communities may in part be due to how disturbance effects are measured for fishes. For lower trophic levels (i.e., periphyton and invertebrates), a range of disturbance measures have been evaluated (e.g., shear stress, particle movement, hydrological) to assess which indices best correlate with community changes (e.g., Clausen & Biggs 1997, Townsend et al. 1997b). Comparisons of both bed movement and flow-related disturbance measures (e.g., Death & Winterbourn 1994,

Townsend et al. 1997b) have generally concluded that bed movement (i.e., the movement of bed substratum of various sizes during high discharge events) indices are better correlated with community changes than flow metrics (i.e., hydrological variables used to describe disturbance regimes in terms of flow variability, flood magnitude or flood frequency). This is presumably because periphyton and invertebrate communities are intimately associated with the stream bed, so when bed substrates are mobilised, these communities are strongly impacted.

Whilst periphyton and invertebrate communities are predominantly benthic organisms, fish species may occupy benthic and/or pelagic habitats, so determining a disturbance metric that accurately predicts changes in fish communities has not been as straight-forward. Almost by default, the effects of disturbance on fish assemblages have been described using flow measures as flow data are often readily available for many streams (e.g., Poff & Allan 1995). However, the usefulness of bed-movement disturbance measures for predicting changes in fish communities has rarely been assessed. Predicting variation in fish communities using only flow-related measures may marginalise the importance of biotic interactions between fish and invertebrates, even though such interactions are a strong determinant of fish communities (e.g., Power et al. 1985, Power 1992a, Nyström et al. 2003, Chapter 3).

Invertebrate community responses may be more tightly coupled to changes in bed disturbance rather than flow regimes, due to shifts in species traits (Death & Winterbourn 1994, Townsend et al. 1997b, Chapter 3). Traits that confer resistance to biotic interactions under more benign conditions (e.g., protective cases or shells) usually increase the susceptibility of a 'protected' species to bed disturbance (Wellborn et al. 1996, Wootton et al. 1996) because their limited mobility (due to the case or shell) means that high rates of crushing mortality can occur when substrates move (Otto & Svensson 1980). Similarly, fish communities may actually respond to bed movement mediated by flow, rather than flow *per*

se (similar to stream periphyton and invertebrates), as bed movement may better reflect changes in habitat and food availability for fish. Thus, a disturbance measure for fish communities should reflect variation in habitat and food (i.e., invertebrates) availability because these are two major factors known to limit fish abundance (Schlosser 1985, Power 1992b).

To assess the effects of flow-related disturbance on stream fish communities and determine which measure(s) of disturbance best predicted variation in fish biomass and community structure, I conducted intensive surveys at 20 sites for fifteen months. Disturbance measures that incorporated some element of bed movement (i.e., tracer particle measures, river disturbance index) were expected *a priori* to be better predictors of fish community variation than flow measures (H_1) because bed-movement measures may better reflect variation in lower trophic levels (i.e., periphyton and invertebrates) that affect fish food supplies and fish habitat availability. Fish biomass and community structure were expected to become more variable as disturbance increased (H_2) because prey resources decline as flow-related disturbance increases (Death & Winterbourn 1994, 1995, Chapter 3), leading to fluctuating fish communities due to species extirpation and recolonisation. Finally, I tested whether the effect of disturbance on fish food availability (i.e., an indirect effect of disturbance) was more important than direct disturbance-related effects to physical habitats used by fish (H_3).

Methods

Study Area

Fish communities were assessed at fifty two sites in Canterbury, South Island, New Zealand from 2005 to 2009 (Fig. 1). During these years, sites were sampled from September (early

spring) through to April (mid-autumn) to avoid periods of low biological activity during winter. Sites were mainly located in high-country catchments that drained into either the Rakaia or Waimakariri River (altitude 480 – 900 m), although five sites were also surveyed on Banks Peninsula (altitude < 50 m). Located on the eastern side of the Southern Alps, a combination of grey sandstone and dark mudstone (commonly called greywacke) dominated high-country catchments (Bradshaw 1977). Variable rainfall in the alpine headwaters of these streams (e.g., 1000 – 5000 $mm \cdot yr^{-1}$, Greenland 1977) means that unpredictable and sudden increases in discharge can occur. In contrast, Banks Peninsula was formed by two overlapping volcanic cones (*c.* six million years ago) which have now been heavily eroded to produce short, steep catchments. Its proximity to the sea means that rainfall on Banks Peninsula rarely exceeds 1500 $mm \cdot yr^{-1}$ and that there is less variation in stream water temperatures. The dominant catchment vegetation in the high-country is a mixture of beech forest (*Nothofagus* spp.) and tussock grasslands, whereas on Banks Peninsula, tussock and exotic grasses are interspersed with pockets of scrub and regenerating podocarp forest. The majority of study sites were grassland streams with surrounding vegetation subject to low-intensity grazing.

Study sites were selected within these catchments (based on prior knowledge) to span a gradient of disturbance (achieved by having sites with contrasting flow regimes e.g., springs, braided rivers, etc.) and encompass a large range in stream size (width: 0.8 – 13.9 m, stream order: 2 – 5). At each site, a single-thread 50 m survey reach was selected which was wadeable and less than 15 m wide (so it could be quantitatively electrofished). Within each reach, there needed to be a 25 m section containing at least one pool, run and riffle habitat for electrofishing. Sites were excluded if they: did not meet these criteria, were fishless, had pH values that may prohibit some species from being present (< 6 or > 8.5) or had high conductivity values (> 150 $\mu S \cdot cm^{-1}$; indicative of potential water pollution in these particular catchments).

Intensive fish surveys assessing fish community responses to disturbance

Fish surveys

To investigate how fish communities varied with disturbance across space and time, a subset of 20 sites (from the 52) were sampled quarterly from July 2008 to July 2009 (five fish surveys in total). This subset of sites was selected based on previous knowledge of the fish communities, physico-chemical conditions and likely disturbance regimes at these locations. Site selection was intentionally non-random so that variation in environmental factors not of interest could be reduced to focus on the influence of disturbance on fish communities. On each sampling occasion, a 25 m reach was quantitatively three-pass electrofished with stop nets (Fig. 1, Plate 2) using a Kainga EFM 300 backpack electrofishing machine (NIWA Instrument Systems, Christchurch, N.Z.) with 300 – 600 V pulsed DC (pulse width ~ 3 ms, 60 pulses s^{-1}), and with the operator moving in a downstream direction towards a 1 m wide push net (mesh size 3 × 2 mm ellipse). Electrofishing in a downstream direction is the most efficient method for capturing fish species in these streams (Jellyman & McIntosh 2010). All captured fishes were anaesthetized with 2-phenoxyethanol, measured [to the nearest 1 mm; fork length (FL) for salmonids and total length (TL) for other species], weighed and released.

Environmental variables

Habitat parameters possibly affecting fish communities were measured either prior to the surveys (e.g., substrate size, altitude) or during each of the five fish surveys (e.g., conductivity, canopy cover; see Appendix 1 for a summary of the major variables). For each survey, five width-depth transects and water chemistry parameters (dissolved oxygen, pH and conductivity) were measured to assess any temporal changes. Air and water temperature (accuracy ± 0·5°C) and stage (i.e., water) height (accuracy ± 1 mm) were measured every

hour for fifteen months (April 2008 – July 2009) using TruTrack® WT-HR 1000 or 1500 (TruTrack, Christchurch, N.Z.) data loggers at all study sites. Loggers were secured to steel y-posts that were set into the stream bed (except at highly disturbed sites where loggers were bolted into bedrock or attached to bridges, see Plate 2). During a large flood, one logger (Hawdon River) was ripped off its bedrock attachment (i.e., by a floating tree) six months after installation. At this site, water height for the remaining nine months was determined from an upper-catchment rainfall gauge (and validated against variation in water height from a logger 20 km downstream[1]) and water/air temperature data were estimated from a nearby logger (Cass River logger, 3 km south).

[1] Waimakariri River @ Esk. This stage height logger is maintained by Environment Canterbury.

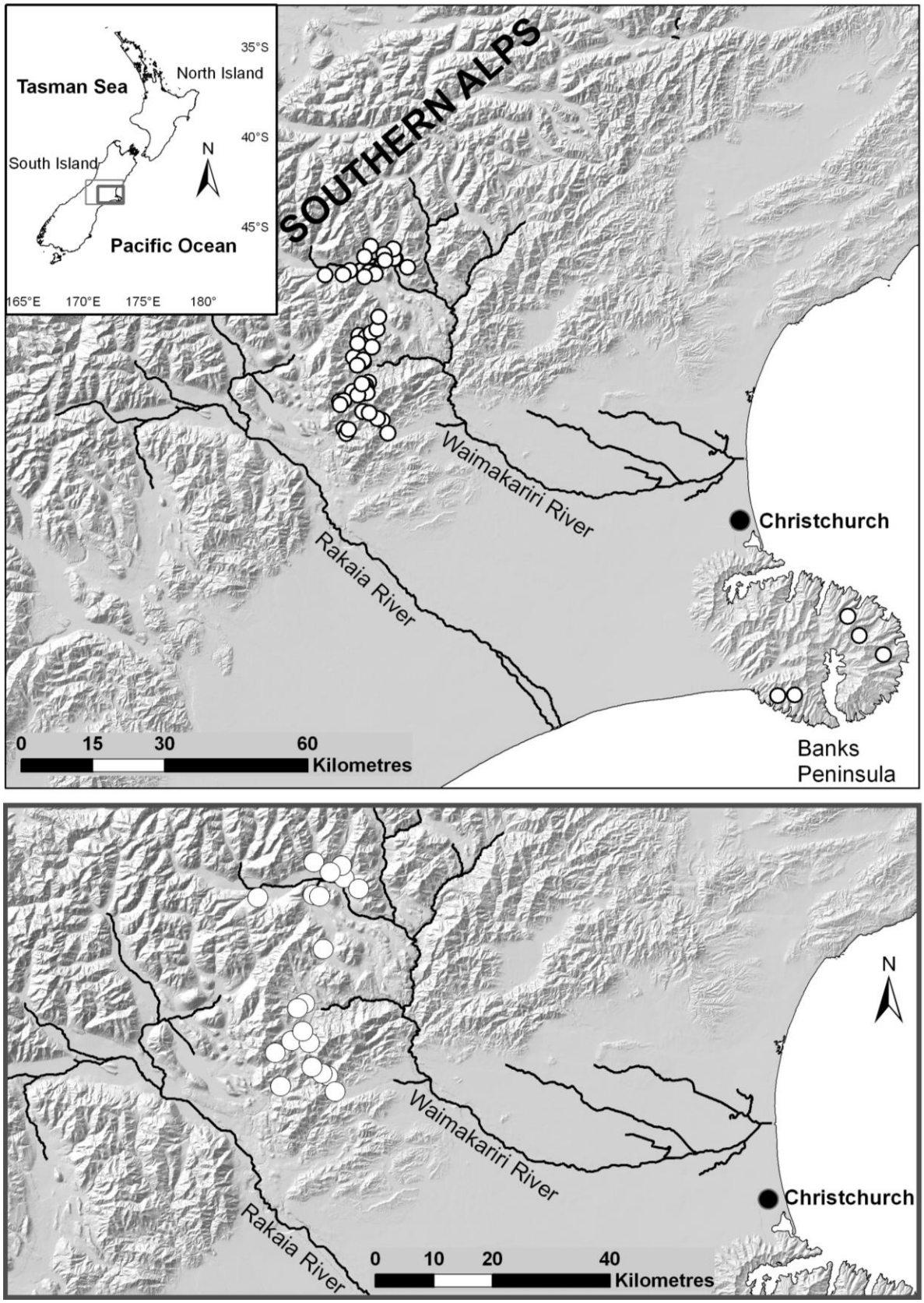


Figure 1. The location (white circles) of the 52 sites from the extensive stream community survey (top) and the 20 sites used in the intensive fish surveys (bottom). The border thickness of each map relates to its position on the map insert. Only major rivers are shown for clarity.

Disturbance measures

Stream disturbance was assessed with a range of flow and channel stability measures to evaluate which index/indices reflected most strongly, variation in fish communities (whichever index was found to be the best predictor of disturbance would be used throughout the thesis research). The disturbance measures were comparable to the seven used by Townsend et al. (1997b) to quantify disturbance effects on stream invertebrates. Stream-bed movement was measured in response to high flow events following the protocol of Townsend et al. (1997b). Painted tracer particles, which corresponded to the 50^{th}, 75^{th} and 90^{th} percentiles of the substratum size distribution, were arranged in five rows (spaced two metres apart) with one particle from each size class randomly assigned to each row (Plate 2). The movement of these particles was monitored on seven occasions (*c.* bi-monthly) from May 2008 to July 2009, and each time, particles that had moved were noted and reset/replaced. Tracer particle movement was used to calculate three disturbance indices: 1) Disturbance intensity – the average proportion of painted rocks that had moved during the seven monitoring occasions; 2) Disturbance frequency – the proportion of the seven monitoring occasions when disturbances greater than a certain magnitude had occurred [the same four categories were used that had been arbitrarily selected by Townsend et al. (1997b): 20, 40, 60 and 80% bed movement]; and 3) Maximum disturbance intensity – the greatest proportion of bed movement that occurred during the monitoring. This tracer particle approach does involve adding new substrates to the stream bed which may bias estimates of natural disturbance levels, and may also produce estimates of mean bed disturbance with large standard errors (Downes et al. 1998). However, it also has a number of advantages over other methods (e.g., critical-tractive force approach) because it is site-specific and produces a direct measure of bed movement, rather than one that is calculated from equations developed for particular substratum sizes under uniform flow conditions (Townsend et al. 1997b).

Stage height was measured at each site using either a 1 m or 1.5 m long (depending on stream size) WT-HR stage logger (Trutrak, Christchurch, N.Z). When most streams were in flood, it was not possible to measure discharge (i.e., calculate an accurate stage-discharge relationship, see Plate 2), therefore, stage-height measurements were used to calculate flow-based indices. Stage-height data reflects variation in stream flow (similar to the actual flow data), so it can be used to produce defensible flow-related disturbance measures. Three flow indices were calculated using stage-height data: 4) Coefficient of variation of stage height (calculated from the water-height data which was recorded every hour during the 15 month study); 5) Maximum stage-height ratio [calculated as (maximum stage – median stage)/median stage)] – a standardised index of the largest flow during the survey; 6) Flood frequency – the number of floods during the survey that were greater than twice the median stage height.

The final disturbance measure was 7) the river disturbance index (hereafter abbreviated to RDI) (Pfankuch 1975). The index estimates disturbance based on 15 categories that evaluate landscape, riparian and stream characteristics (e.g., landform slope, vegetative bank protection, channel capacity, amount of deposition, etc.). The observer visually grades each category and the scores are summed to give an overall index score (RDI range: 38–152). Small numbers indicate the waterway is stable, whereas a larger number signifies the waterway is physically unstable/highly disturbed.

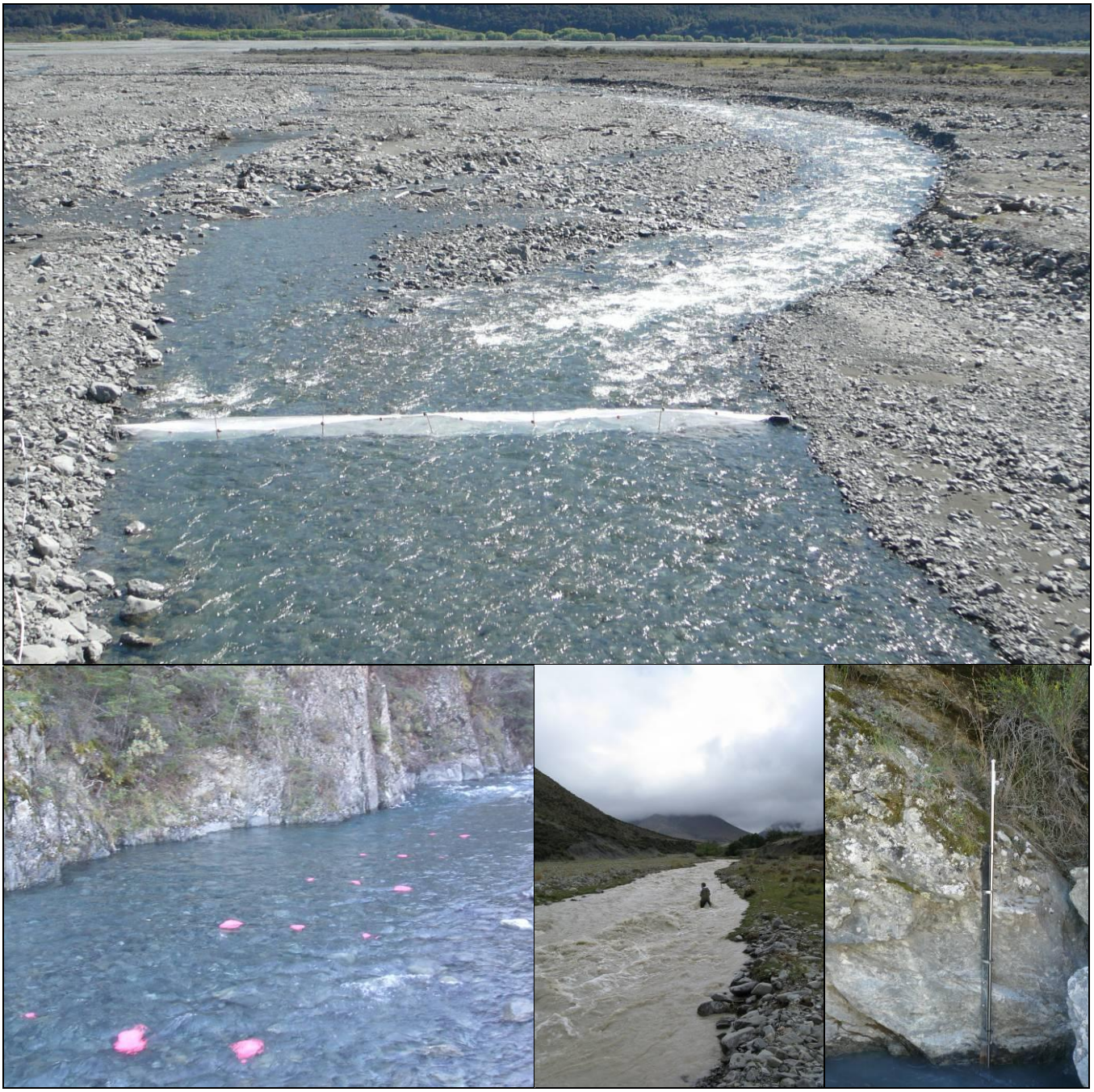


Plate 2. A large, disturbed site (Bruce Stream) that was quantitatively electrofished during the intensive surveys (top). Painted tracer particles *in situ* (bottom left). A site in flood that was flowing too fast through the thalweg to attempt a discharge transect (bottom middle). A WT-HR stage logger that was bolted into bedrock at a disturbed site (bottom right).

Extensive stream community survey

To investigate the relationship between disturbance, invertebrate and fish communities, a 50 m reach was sampled at 52 sites from April 2005 (autumn) to June 2009 (winter). At each

site, both invertebrate and fish communities were sampled in the reach and a disturbance (measured using the RDI; index range for sites: 50 - 141) assessment conducted. Fish communities were sampled in a 25 m section of the reach using the methods previously described. To sample invertebrates, five Surber samples (0.0625 m^2, mesh size 250 µm) were taken within the reach to determine invertebrate biomass. One sample was taken every 10 m in riffle or run habitat. Invertebrates were preserved in 90% ethanol, and sorted and identified in the laboratory at a magnification of ×10. Aquatic invertebrates were identified to either genus or species level (except Chironomidae, which were identified to sub-family) using the keys of Winterbourn et al. (2000). Ash-free dry mass (AFDM) of each group was calculated by air drying for at least 48 h at 50 °C, followed by ashing at 550 °C for 4 h. At each stage of the drying and ashing process, samples were weighed to the nearest 0.1 mg on a Mettler Toledo AB204-S balance (Küsnacht, Switzerland).

Data analysis

Intensive surveys

Disturbance measures were initially subjected to principal components analysis (PCA) in Systat 10. A correlation matrix was used to extract a limited number of independent and uncorrelated factors that best described disturbance. Axes that had eigenvalues greater than one were retained (Dillon & Goldstein 1984). PCA factors and individual disturbance measures were then regressed against fish biomass (log-transformed) to determine the best predictor/s of fish community biomass (with the inclusion of PCA factor one there was effectively eight disturbance measures) (to test H_1).

A path analysis was conducted to assess whether the effect of disturbance on fish biomass was due to flow variability (i.e., direct effect) or bed movement mediated by flow variability (i.e., indirect effect). This analysis allowed the direct, indirect and total (i.e., flow

variability and bed movement) effects of disturbance on fish biomass to be disentangled by comparing the relative strengths of direct versus indirect pathways. Path analysis is superior to ordinary least-squares methods (i.e., regression or correlation) because it can quantify direct effects on a response variable caused by variation in a predictor variable, while removing effects of other predictor variables (Mitchell 2001, Yee & Juliano 2007). The fitted model produces standardised path coefficients for all paths (i.e., direct and indirect effects) that range between 0 and ±1. These path coefficients are equivalent to standardised regression coefficients since larger path coefficients indicate a stronger relationship but have the advantage of specifying whether the relationship between the predictor and response variable has a positive or negative slope. In the analysis, direct and total indirect (e.g., the product of flow variability–bed movement and bed movement–fish biomass coefficients) path strengths, as well as their difference, were estimated; 95% confidence intervals were generated for each estimate by bootstrapping (n = 1000 iterations). Bootstrapped confidence intervals that include zero within their range indicate a non-significant path. All response and predictor variables, except bed movement, were $\log_{10}$ or $\log_e$-transformed to meet the assumptions of maximum likelihood estimation and multivariate normality. Analyses were completed using the SEM package in R (R Development Core Team 2009).

To evaluate which of the five factors (i.e., disturbance, habitat size, substrate size, water temperature and canopy cover) had the most influence on fish community biomass, regression analysis was conducted. Coefficients of determination (R^2) were used to identify the factor which best predicted fish community biomass (calculated as mean biomass from the five surveys).

The effect of disturbance on fish communities was evaluated by assessing both spatial and temporal changes in species biomass at each stream for the five sampling occasions (H_2). Temporal variability in fish biomass was assessed by calculating the coefficient of variation

(CV) for biomass at each site over the five surveys, and regressing this data against disturbance measures. To evaluate both predictability and variability in community structure, the biomass of each fish species (log-transformed to downweight species with a large body size) was used to generate a Bray-Curtis dissimilarity (resemblance) matrix which was then subjected to ordination using non-metric multidimensional scaling (NMDS) (two data points were excluded because no fish were recorded during these surveys). The NMDS was given 25 random starts in both two and three dimensions. To simplify later analysis, I retained only two dimensions, as the third dimension resulted in only a minor reduction in the ordination stress value (0.14 vs 0.09). Scores from the two NMDS axes were averaged for each site to analyse whether the structure of fish communities responded predictably to changes in disturbance. Variation in community structure between sites was analysed using PERMDISP, which tests for heterogeneity in the average dissimilarities of points from the central location (i.e., centroid) of their group (Anderson 2004). Significance was tested ($P < 0.05$) after 999 permutations. To assess whether variation in fish community structure was influenced by disturbance, I extracted an index of multivariate dispersion (IMD) for each site from the NMDS, to use in a regression analysis. The IMD was calculated by averaging the dispersion distance for each of the five temporal surveys from its site centroid.

Extensive surveys

The influence of invertebrate biomass (i.e., food availability) on fish community biomass was assessed over multiple years using an analysis of variance (ANOVA) with year as a random blocking factor. Following this analysis, the relative importance of disturbance-related changes to physical habitat and food availability for fish communities was determined. A path analysis was used to separate the effect of disturbance on fish food supply (i.e., indirect

disturbance effect) from the physical (i.e., direct) effect of disturbance, so that the relative importance of the two components on fish biomass could be compared (testing H_3).

Results

Measures of flood-related disturbance for fish

To select a bed movement disturbance frequency threshold for use in analyses (i.e., disturbance measure 2), disturbance intensity was plotted against four bed movement disturbance frequency thresholds. These thresholds were based on the proportion of the seven sampling periods where a particular disturbance intensity (20, 40, 60 or 80% of tracer particles moved) was exceeded. However, there were significant relationships between disturbance intensity and frequency, irrespective of the threshold used to calculate disturbance; all regressions were highly significant ($P < 0.0001$) with the coefficients of determination (R^2) 0.87, 0.94, 0.93, 0.95, for 20, 40, 60 and 80% of the bed moved, respectively (Appendix 2). As there was very little variation between the 40 – 80% disturbance frequency regressions, frequency data based on the 40% bed-movement threshold was used in analyses because data points were most evenly distributed across the frequency gradient for that threshold (see Appendix 2). Furthermore, the three disturbance measures based on bed movement were highly intercorrelated ($r = 0.85 – 0.97$). Bed-movement measures were also correlated with flow-based indices ($r = 0.49 – 0.76$), and similar to bed-movement measures, flow-based indices were also intercorrelated ($r = 0.69 – 0.81$). RDI correlated more strongly with bed-movement measures ($r = 0.65 – 0.94$) than with flow-based indices ($r = 0.59 – 0.80$).

One PCA factor explained 75% of the variance for the seven disturbance indices, and this was the only factor with an eigenvalue greater than one. Each of the seven disturbance indices was strongly correlated with factor one, but the highest loadings were with disturbance intensity (0.951) and the RDI (0.936). Regression analysis showed there was a close relationship between RDI and disturbance intensity based on the proportion of rocks moved (Fig. 2).

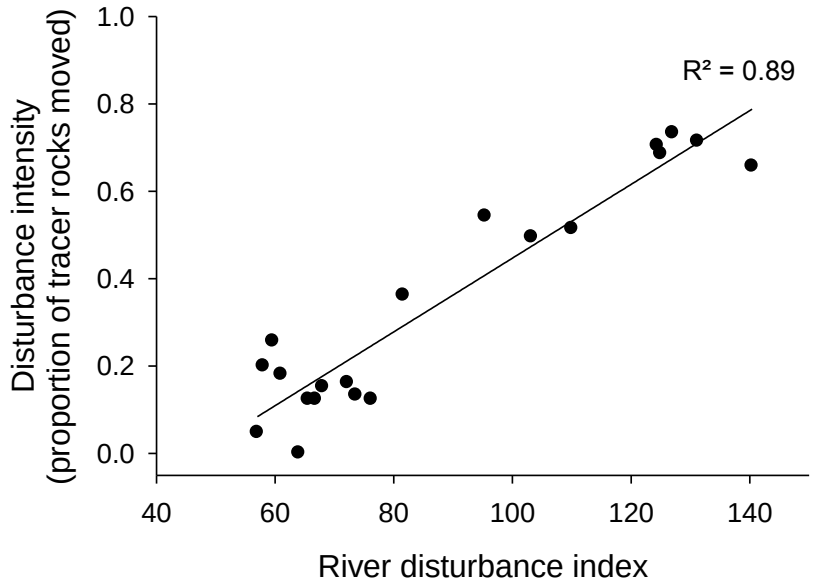


Figure 2. The correlation between the river disturbance index and the proportion of tracer rocks moved (i.e., the two variables with the highest loadings on PCA factor one).

The total biomass of fish communities declined significantly as disturbance increased for all seven disturbance measures and PCA factor one in the intensive surveys (Fig. 3). Flow-based indices did not account for as much variation in fish biomass as the disturbance measures that incorporated some component of bed movement (i.e., painted tracer particle measures and the RDI). PCA factor one was strongly correlated with all disturbance indices, but both disturbance intensity and the RDI explained more variation in fish biomass than PCA factor one (Fig. 3). Although disturbance intensity was a slightly better predictor of fish biomass than RDI, RDI was used in subsequent analyses because both variables were strongly related (Fig. 2, and see Table 1 in the next section).

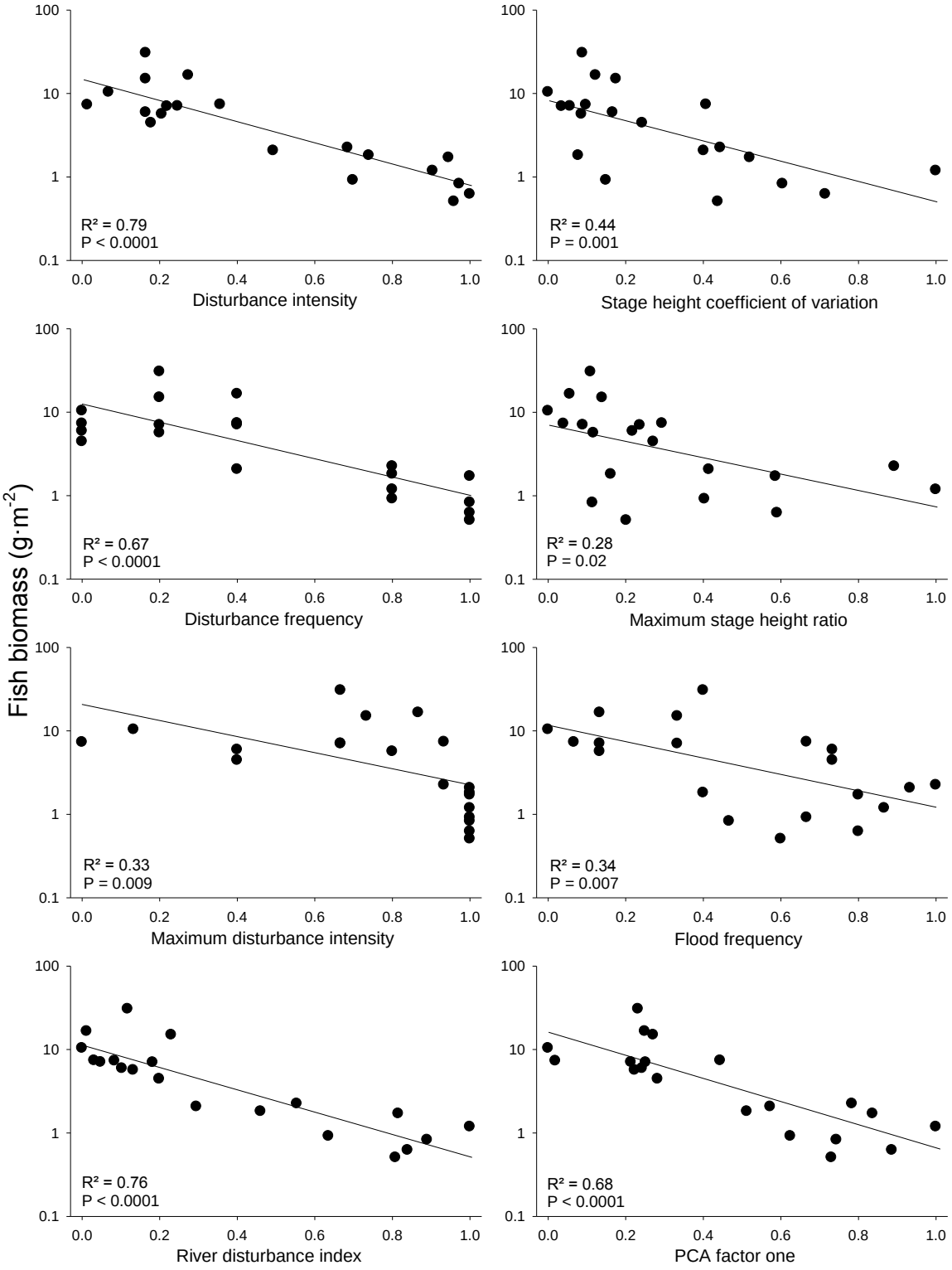


Figure 3. Relationships between fish biomass and all eight disturbance measures assessed. Data are average biomass values from the five intensive surveys at each of the 20 streams. All disturbance measures were scaled between 0 and 1 to allow easy comparison. The ranges of values for each disturbance measure were: disturbance intensity, 1 – 73%; disturbance frequency, 0 – 83%; maximum disturbance intensity, 1 – 100%; stage height CV, 14.6 – 108.4%; maximum stage height ratio, 1.8 – 9.8; flood frequency, 0 – 15; river disturbance index, 57 – 141; PCA factor one, -4.3 – 3.6.

In the first path analysis, there was a significant total effect of flow variability on fish biomass using the intensive survey data, which was dominated by the significant indirect path linking flow variability to fish biomass via bed movement (Fig. 4). For the indirect path, the path coefficient for the direct link between flow variability and bed movement was significant and positive, whereas, the direct link from bed movement to fish biomass was significant and negative. The direct path between flow variability and fish biomass was relatively weak and not significant because the indirect path comprised >99% of the total effect of flow variability on fish biomass. Thus, the effect of disturbance on fish biomass was almost entirely due to its influence on bed movement.

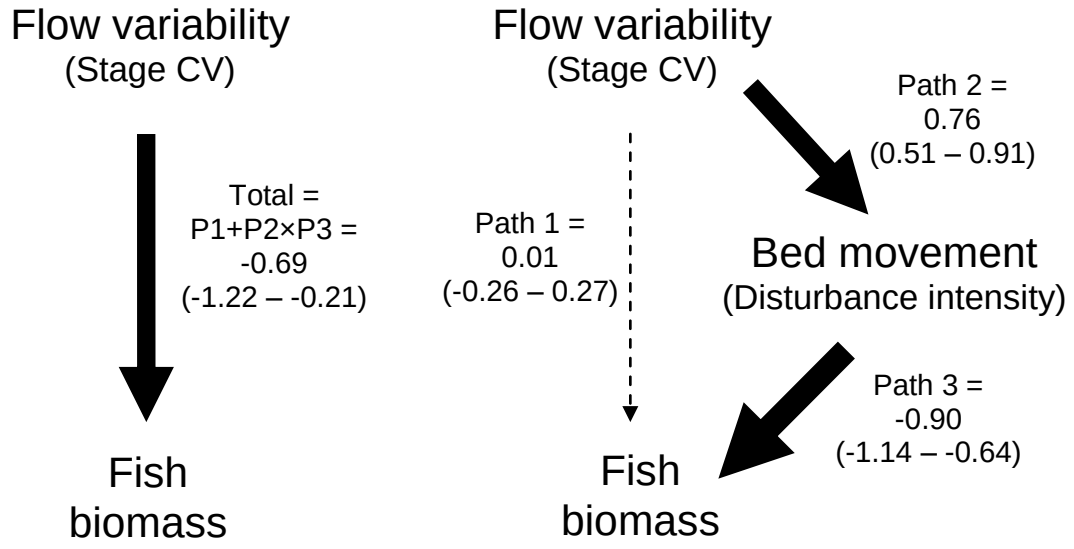


Figure 4. Path analysis of relationships between flow variability (stage CV), bed movement (disturbance intensity) and fish biomass from the intensive surveys of 20 streams. This analysis separates the total effect (left) from the direct and indirect effects (right). Arrows point from predictor to response variables and the thickness of the arrows indicates the magnitude of the path (e.g., P1) weights. Solid lines indicate significant effects, whereas dashed lines indicate non-significant effects. Numbers are mean path coefficients with bootstrapped 95% confidence intervals shown in parentheses.

Of the five factors most likely to influence fish biomass (i.e., disturbance, habitat size, water temperature, substrate size and canopy cover), disturbance explained twice as much variation in fish biomass than any other variable (disturbance, $R^2 = 0.76$; canopy cover, $R^2 = 0.38$; other factors $R^2 < 0.20$).

Spatial and temporal variability in fish communities across a flood-related disturbance gradient

Temporal variability in fish biomass increased significantly with stream disturbance (regression: $R^2 = 0.58$, $P < 0.001$), and across the disturbance gradient, there was more than a three-fold change in temporal biomass variability (Appendix 3). Thus, some streams experienced very large changes in fish biomass over the course of the study, whereas biomass in other streams was quite consistent.

A total of eight fish species were captured during the intensive surveys, and variability in fish community structure depended on the stream (Fig. 5a). NMDS axis 1 was correlated with compositional changes in fish species biomass, particularly trout biomass (Appendix 4), whereas NMDS axis 2 was positively correlated with total fish biomass and negatively correlated with disturbance (Appendix 4, Fig. 6a). The significant negative correlation between NMDS axis 2 and disturbance indicated that fish community structure changed predictably along the disturbance gradient with disturbed communities dominated by alpine galaxias and stable communities by longfin eels.

The degree of separation between sites was highly variable in ordination space, but an ANOVA test of multivariate dispersion distances (i.e., IMD) using the NMDS showed that samples from disturbed sites (i.e., these with RDI > 110) were significantly more dispersed in ordination space than those from stable sites (i.e., those with RDI < 80) (ANOVA from PERMDISP analysis: $F_{19, 99} = 6.05$, $P = 0.001$). Thus, although there was high community

overlap between stable and disturbed sites in ordination space, the biomass and composition of disturbed sites (i.e., those with larger RDI scores) were much more variable than at stable sites (e.g., Figs 5b, c). This was also evident in a regression of IMD against disturbance (Fig. 6b) because as disturbance increased, fish community structure was significantly more variable (R^2 = 0.62, P < 0.0001). Sites that were stable (RDI < 80) with less variable community structure also had significantly higher fish biomass than more disturbed sites (one-way ANOVA: $F_{1, 19}$ = 66.27, P < 0.0001, Fig. 6). Therefore, disturbance strongly affected both the predictability and temporal variability of fish community structure.

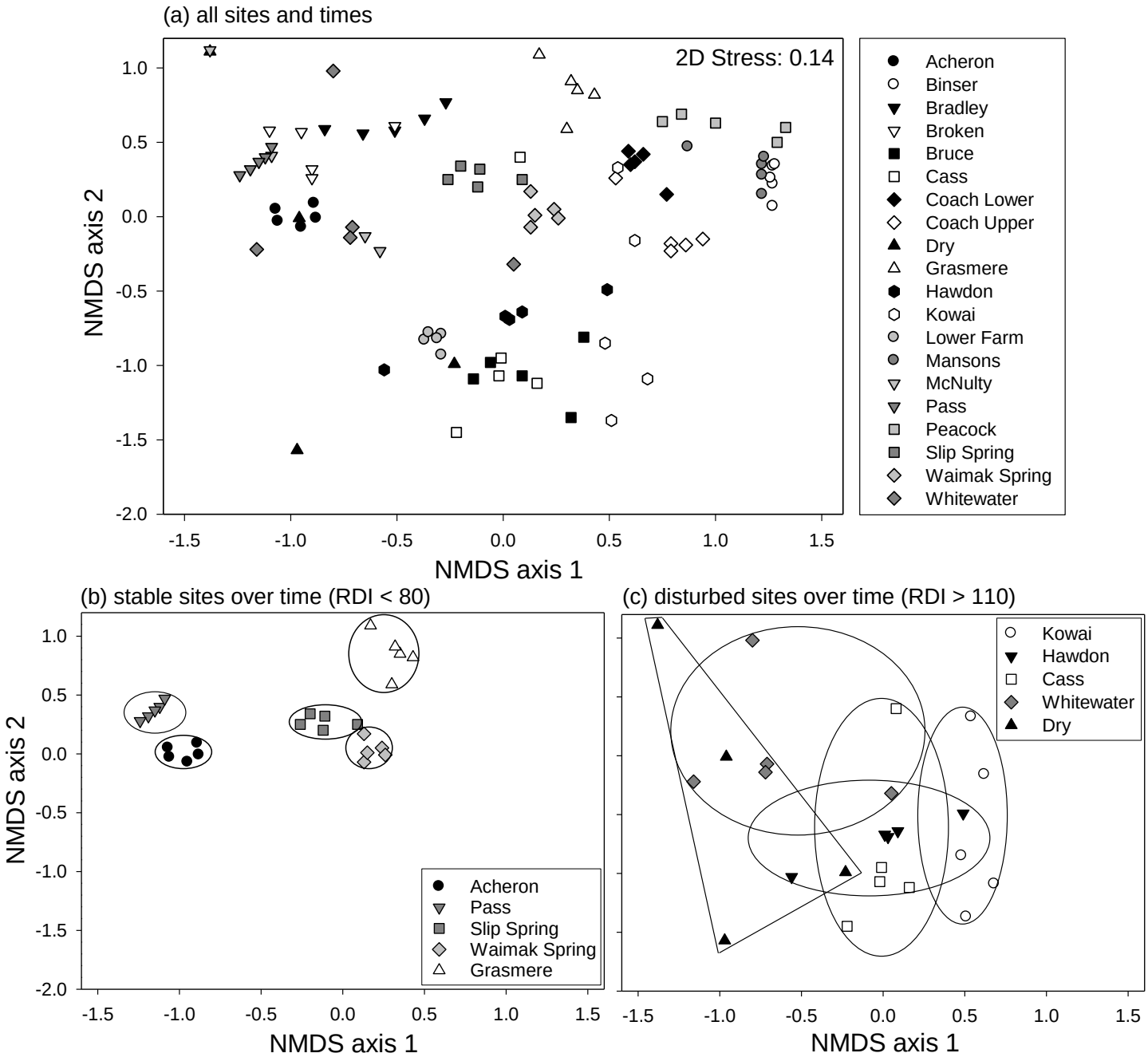


Figure 5. Non-metric multidimensional scaling (NMDS) ordination of a Bray Curtis dissimilarity matrix of quantitative fish community composition for the 20 sites sampled during the intensive surveys (a). A comparison of community dispersion between stable (b) and disturbed sites (c) is also shown, but only five sites of each disturbance-type are presented for clarity.

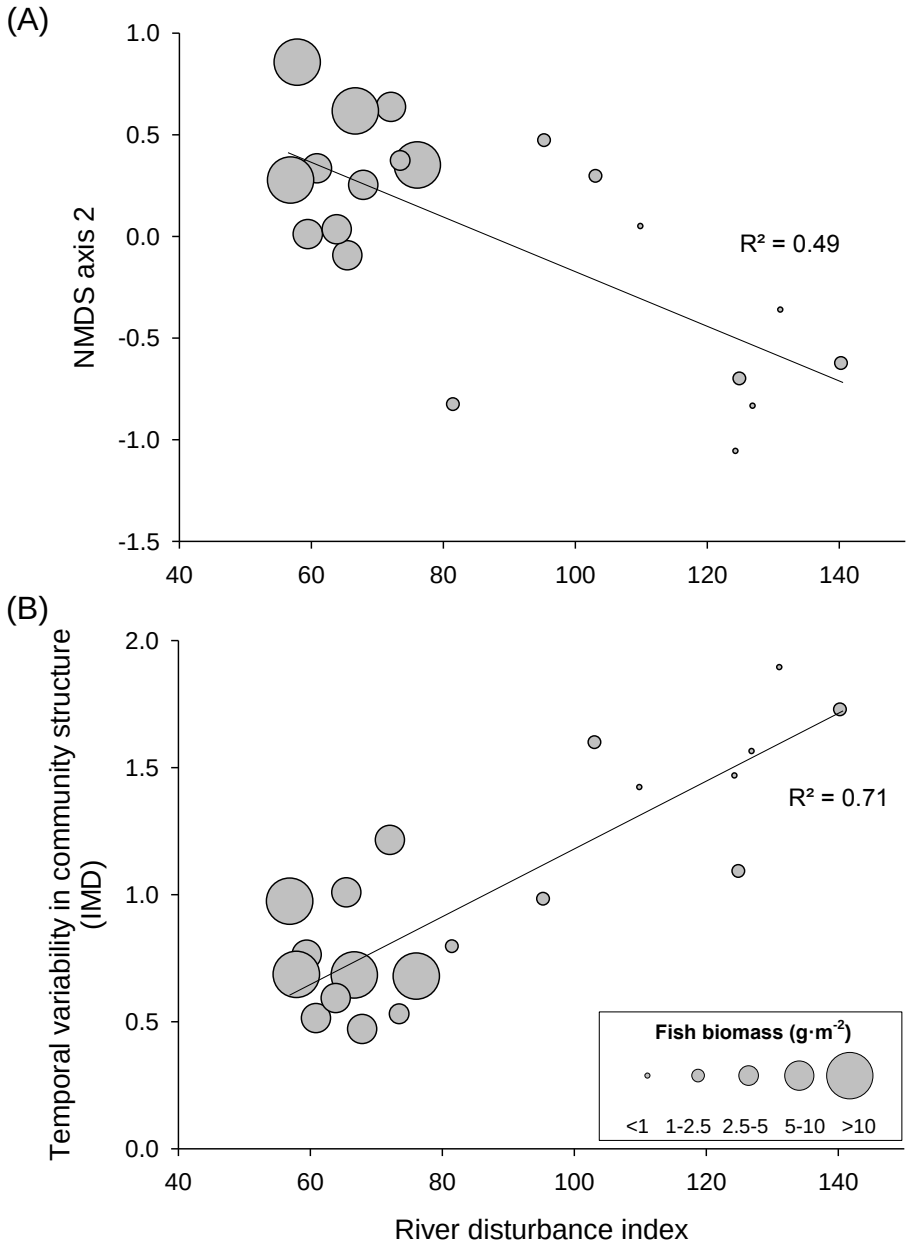


Figure 6. The relationship between disturbance and (a) mean non-metric multidimensional scaling (NMDS) axis two, and (b) mean variability in fish community structure measured by the index of multivariate dispersion (IMD). Mean NMDS dimensions were calculated over the five replicate surveys for the 20 intensive fish survey sites, and the IMD was calculated as the average vector length between replicates for an ordination site centroid (see methods). The area of the circles indicates the mean fish biomass (see legend) that was present at each site over the survey period.

The regression coefficients for all linear models evaluating fish community responses to disturbance measures were ranked to find the best measure of disturbance for fish communities. A comparison using four fish community characteristics (biomass, biomass

variability, community structure and community variability) showed that measures with a strong focus on bed movement (e.g., RDI or painted tracer particles) were generally better predictors of fish communities than flow-based indices (Table 1). The RDI was consistently in the top two measures for all fish community responses and was subsequently ranked as the top disturbance measure (Table 1). As a result, the RDI was chosen as the index for use in all disturbance-related thesis research. Disturbance intensity was the top predictor of fish biomass, but across all responses ranked as the second best measure of disturbance on fishes. Stage height CV (a flow-based measure) was also in the top two predictor variables for biomass variability and community structure but ranked 4th across all responses.

Table 1. The relationship between the eight disturbance measures and four measures of fish community characteristics. The values in the table are coefficients of determination (R^2) derived from linear regression analyses. The top two measures explaining the most variation in each column are bolded.

Disturbance measure	Biomass	Biomass variability (CV)	Community structure (NMDS axis 2)	Community variability (IMD)	Average (rank)
Disturbance intensity	**0.79**	0.45	0.47	**0.64**	**0.59 (2nd)**
Disturbance frequency	0.67	0.40	0.33	0.56	0.49 (5th)
Max. disturbance intensity	0.33	0.22	0.15	0.24	0.24 (8th)
Stage height CV	0.44	**0.57**	**0.54**	0.47	0.51 (4th)
Max. stage height ratio	0.28	0.25	0.20	0.34	0.27 (6th)
Flood frequency	0.34	0.08	0.33	0.26	0.25 (7th)
River disturbance index	**0.76**	**0.57**	**0.49**	**0.71**	**0.63 (1st)**
PCA factor one	0.68	0.47	0.47	0.61	0.56 (3rd)

Were fish communities limited by food- or habitat-related factors?

As the biomass of aquatic invertebrates increased, so did the biomass of stream fishes at the 52 sites sampled in the extensive survey (randomised block ANOVA: $F_{1,\ 49} = 10.26$, $R^2 = 0.58$, $P < 0.0001$). The positive slope and y-intercept of this fitted relationship ($y = 2.28x^{0.96}$) indicated that a 1 g increase in invertebrate biomass (g AFDM·m^{-2}) was linked to 2 g of extra fish biomass (g wet weight·m^{-2}) being supported (Appendix 5).

The path analysis described previously (Fig. 4) showed that there was a significant link between bed disturbance and fish biomass. Results from the extensive one-off stream community survey were used to further elucidate the food-related and physical habitat-related components of the bed disturbance effect. The second path analysis evaluated the relative importance of the direct path from bed disturbance to fish biomass compared to the indirect pathway involving the food of fish (disturbance→invertebrates→fish). The total effect of disturbance on fish biomass was significant and negative, and fish biomass responded similarly to both direct and indirect paths (Fig. 7). Both paths significantly affected fish biomass, with the direct and indirect paths comprising 55% and 45% of the total effect, respectively. Thus, physical disturbance of the bed by itself, and the deleterious effects of bed disturbance on fish food supplies were both involved in disturbance-related reductions in fish biomass.

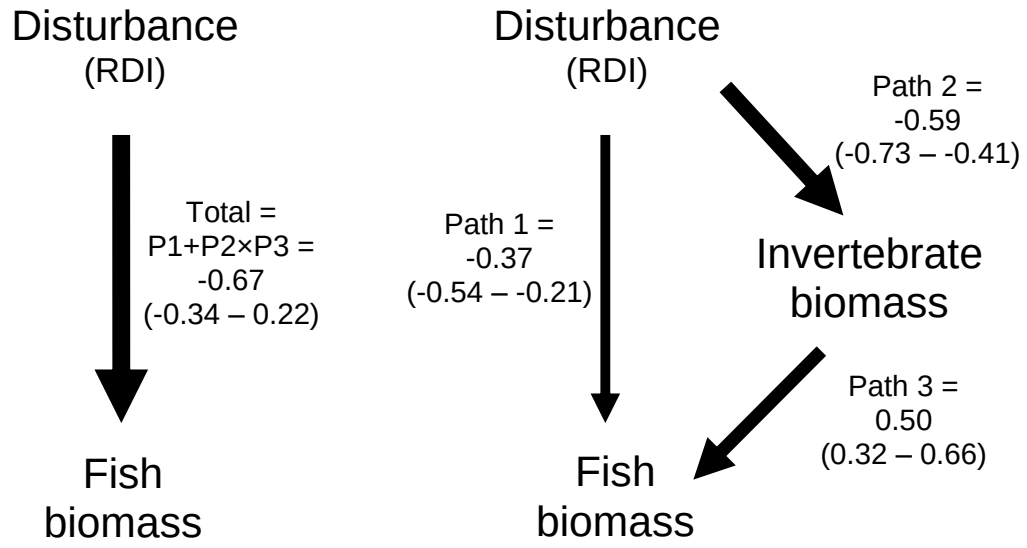


Figure 7. Path analysis of relationships between disturbance (RDI), invertebrate biomass and fish biomass from the extensive stream community survey. This analysis separates the total effect (left) from the direct and indirect effects (right). Arrows point from predictor to response variables and the thickness of the arrows indicates the magnitude of the path weights. Solid lines indicate significant effects, whereas dashed lines indicate non-significant effects. Numbers are mean path coefficients with bootstrapped 95% confidence intervals shown in parentheses.

Discussion

A range of methods measuring the intensity, severity, frequency and predictability of disturbance have been developed for stream communities (Poff & Ward 1989, Death & Winterbourn 1994, Townsend et al. 1997b), but rarely have disturbance measures other than hydrological indices been used to predict variation in fish assemblages. I assessed a range of disturbance measures and found that bed-movement measures were better predictors of fish communities than simple flow-based indices. This was because changes in fish biomass and community structure were largely due to bed movement, mediated by flow variability, with effects of bed movement linked to influences on both physical habitat and fish food supplies. Below I examine the implications of these findings, and outline how they can be applied in management of stream communities.

Disturbance measures as predictors of fish communities

Many researchers have attempted to determine the best measure of disturbance for stream ecosystems, concluding that metrics need to characterise disturbance events by encapsulating spatial and temporal variability in flow regimes (e.g., Resh et al. 1988, Poff & Ward 1989, Sabo & Post 2008). However, studies that have compared flow and bed-movement disturbance effects on benthic invertebrates (e.g., Death & Winterbourn 1994, Townsend et al. 1997b) have found that bed-movement measures (including the RDI which has a major bed stability component) were better predictors of community responses to disturbance than flow-based indices. In stream fish communities, variation in disturbance has been inferred from indices derived mainly from flow, although the use of bed-movement indices to predict changes in fish community structure has received little attention. My results suggest that even though flow and bed movement are strongly correlated, fish communities are more likely to respond to changes in bed movement (mediated by flow), rather than responding directly to

flow. My results do not contradict the numerous studies have found that flow variability has important effects on fish communities (e.g., Grossman et al. 1982, Jowett 1990, Poff & Allan 1995). The intent of this disturbance research was not to marginalise the importance of flow effects on fish communities (as flow was still a significant predictor of fish responses in many analyses). My goal was instead to assess whether the current approach to estimating disturbance effects on fish communities could be improved. Despite the relatively simplistic flow measures, my results clearly showed that measuring disturbance due to bed movement significantly improved the accuracy of fish community analyses, and below I suggest how this new knowledge can be applied to advance our understanding of community responses to disturbance.

Whilst disturbance-induced variation in bed movement may be more biologically meaningful for fish communities than flow indices, such measures need to be able to be applied to existing and future data sets if they are to be of practical use. Measuring bed-movement variability (i.e., using painted tracer particles) has one major disadvantage over flow metrics which is that it is time intensive, requiring constant trips to field sites. In contrast, flow data can readily be obtained once stage recorders are installed and calibrated. One solution may be to derive a site-specific bed movement-flow variability curve (*sensu* Duncan et al. 1999) so that flow data can then be used to estimate bed movement and predict stream community responses with improved accuracy. It would be particularly interesting to assess whether the few studies that have been able to quantify the effects of flow disturbance on fish communities for periods greater than a few years (e.g., Poff & Allan 1995) would be improved by estimating flow-mediated variation in bed movement.

As an alternative to intensive bed-movement measures, the RDI (which gives a quick, reach-scale assessment of channel stability) can provide an excellent disturbance measure that is strongly correlated with flow-based indices, but particularly with direct measures of bed

movement. The RDI (commonly referred to as Pfankuch's index) has been criticised for being subjective and prone to observer bias (Duncan et al. 1999). However, the stream bed component of the index and/or the full index has previously been found to have a strong relationship with other disturbance measures (Death & Winterbourn 1994, Townsend et al. 1997b, McIntosh 2000a). I found it to be the best overall predictor of disturbance-induced changes in fish communities across a range of response variables, so the RDI can be defensibly used as a surrogate for direct bed-movement measures, offering trained researchers a quick but accurate method for predicting the disturbance regime experienced by a particular stream fish community.

The responses of stream biota to variation in disturbance

Flood-related disturbance events can result in high levels of fish mortality, especially in smaller fishes (Hayes 1995, Jellyman & McIntosh 2010), although the response of fish abundance to flooding is often species specific (Jowett et al. 2005). Fish communities vary in their response to disturbance, but they should be more persistent in stable sites compared to those subject to unpredictable floods (Grossman et al. 1982). My results showed that fish biomass and community structure were much less temporally variable at stable sites compared to disturbed streams, which is consistent with findings from North American fish communities (e.g., Grossman et al. 1982). I expected the temporal variability of fish biomass and community structure to increase as streams became more disturbed, because whilst invertebrate communities may recover quickly from disturbance events due to traits such as short life cycles and rapid growth (Scrimgeour et al. 1988, Wallace 1990), fishes are usually slow to recolonise once extirpated. This increased variability is probably linked to both the successional processes that need to occur following a disturbance (i.e., algal growth and invertebrate recolonisation) before significant fish communities can re-establish (Fisher et al.

1982, Taylor & Warren 2001), and the traits of fish species to tolerate particular environmental conditions (e.g., short life history and small body size for fishes in disturbed streams).

Variation in species traits can strongly shape community structure across natural disturbance gradients because predatory species are adapted to exploit a particular set of conditions (i.e., habitat types and prey species) across this gradient (Wellborn et al. 1996). For example, traits that confer a competitive advantage in stable habitats (e.g., large body size in longfin eels) may disadvantage a species in more disturbed environments (these conditions generally favour fishes with small, slender body shapes e.g., alpine galaxias). Thus, changes in species traits across the disturbance gradient may partially explain why variation in fish biomass and community structure increased with disturbance and why these changes were highly predictable both spatially and temporally. To some extent, these results probably also reflect a limited species pool comprised mainly of generalist predatory fishes (McIntosh 2000, McHugh et al. 2010), because the same fish species can occupy both stable and disturbed habitats (as indicated by the high degree of community overlap in the NMDS) albeit at varying abundances. The abundance of generalist predators usually decreases in disturbed environments because resource specialists have traits that allow them to exploit these harsh habitats (Wilson et al. 2008). Therefore, fish communities with a high proportion of these generalist fishes would be expected to exhibit increasingly variable biomass and community structure as habitats became more disturbed. Because the abundance of these generalist fish species decreases with disturbance, and more specialised species increased in abundance (e.g., alpine galaxias, Appendix 3), the change in community structure with disturbance was predictable. Thus, even though the intensity and frequency of disturbance events in these catchments is generally unpredictable (Winterbourn et al. 1981), stochastic environmental factors still result in highly predictable fish communities. Lepori & Malmqvist (2007)

similarly found that changes in invertebrate community structure were predictable across the disturbance gradient, concluding that disturbance effects on basal resources partially explained the predictability of community structure. I would suggest that in addition to the observed fish species effect, a very similar resource-consumer interaction (i.e., invertebrate-fish) was likely to influence fish communities in my study, with changes in the trophic structure and biomass of invertebrate assemblages further contributing to the predictable structuring of fish communities. This concept is tested in Chapter 3.

As aquatic invertebrates are the primary food resource for most temperate stream fishes, it is not surprising that strong predatory interactions have been reported between fish and invertebrates from many stream systems (e.g., Power et al. 1985, Huryn 1998, Nyström et al. 2003). Despite this, the importance of biotic interactions in structuring fish communities has been somewhat overlooked due to the numerous studies that have found significant effects of flow variability on fishes (e.g., Jowett 1990, Poff & Allan 1995). Such research has often focussed strongly on physical habitat changes due to disturbance, with much less attention on fish food supply. However, as disturbance can affect the abundance and traits of invertebrate communities (Death & Winterbourn 1994, Townsend et al. 1997b), fish may also respond to variation in prey communities as well as disturbance-induced changes to physical habitat. My second path analysis showed that disturbance-related reductions in fish biomass were due to both physical disturbance of the bed itself and the deleterious effects of bed disturbance on fish food supplies. Whilst both physical habitat and food-related disturbance effects probably contribute to fish leaving a stream reach, this analysis indicated that changes in food availability accounted for almost half of the variation in the model. Disturbance research on stream fishes has often ignored the importance of food availability, with the underlying assumption that by quantifying changes in fish habitat variation in fish food supply will be incorporated. However, my research suggests that changes to both components

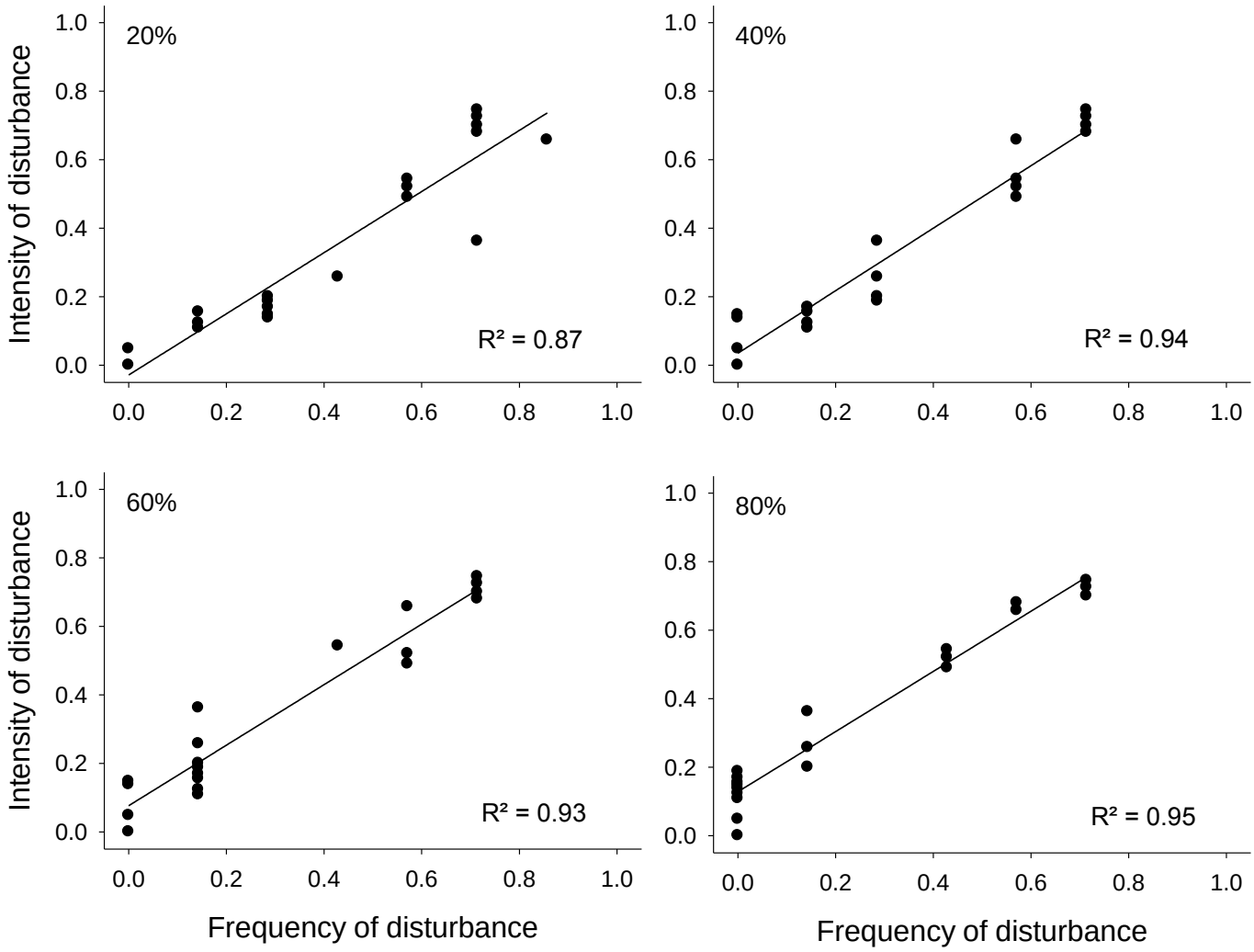
(i.e., physical habitat and food supply) need to be quantified to fully understand how fish communities will respond to disturbance.

As the frequency and intensity of climatic events causing disturbance are predicted to increase in coming years (IPCC 2001), research that addresses how communities respond to variation in disturbance will be increasingly required. Disturbance can have direct and indirect effects on communities, so understanding which pathway(s) is actually influencing species assemblages is often complex. Unravelling this complexity requires accurate disturbance measures so that variation in community responses due to additional factors is reduced. My results suggest that such measures should be based on bed movement not flow variability because bed movement determines not only the community structure of lower trophic levels (e.g., Death & Winterbourn 1994, Townsend et al. 1997b) but also that of fish communities via many of the same mechanisms (i.e., habitat and food availability). Furthermore, as my research has also shown that invertebrate biomass is a major determinant of fish abundance (Appendix 5), I would argue that a greater recognition of the importance of predator-prey interactions in structuring fish communities is required to advance our understanding of disturbance effects.

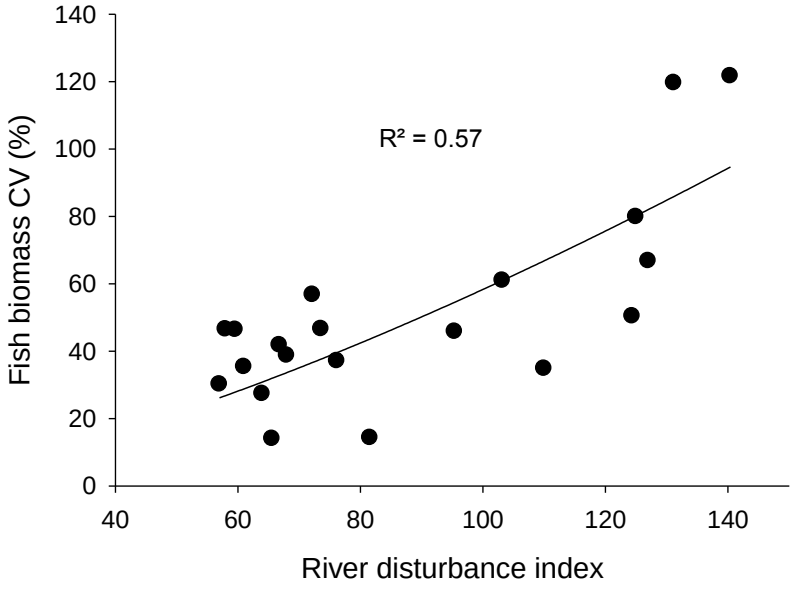
Appendix 1. Characteristics of the 20 stream sites in the intensive survey. Water chemistry, temperature and habitat size (i.e., stream cross-sectional area) measures are averages for the survey period.

Site	Altitude (m a.s.l)	Distance to Sea (km)	Catchment Size (km^2)	Habitat size (m^2)	Width (m)	Max Depth (m)	Substrate size (d_{50})	Water Temp (°C)	Air Temp (°C)	pH	Conductivity (μS_{25} cm^{-1})	Dissolved O_2 (mg L^{-1})	Canopy Cover (%)
Acheron River	823	110.2	10.5	0.56	2.35	0.46	45	6.8	6.9	7.1	61	11.2	10
Binser Stream[1]	536	131.3	4.2	0.30	2.31	0.33	100	6.4	6.8	7.4	72	12.6	20
Bradley Stream[1]	682	116.7	2.3	0.31	2.15	0.4	130	7.9	7.1	8.1	141	11.9	5
Broken River	659	116.4	31.8	1.26	4.90	0.57	57	7.0	7.1	7.5	66	13.0	0
Bruce Stream	627	147.5	28.5	1.50	7.08	0.45	80	6.6	7.4	7.4	95	12.3	0
Cass River	576	136.5	41.3	0.89	4.44	0.41	80	7.3	7.4	7.3	60	11.8	0
Coach Stream-Lower	625	96.1	7.0	0.37	2.62	0.31	78	6.9	7.6	7.3	68	11.3	20
Coach Stream-Upper	692	97.3	3.0	0.24	1.41	0.43	65	7.6	8.1	7.4	103	11.2	10
Dry Stream	758	121.2	6.1	0.16	1.80	0.31	50	7.7	7.2	7.8	55	12.0	0
Grasmere Stream	570	136.0	28.5	1.06	2.89	0.76	70	8.9	8.2	7.1	90	10.7	5
Hawdon River	576	138.2	79.8	2.19	9.76	0.51	60	6.4	7.8	7.4	75	11.3	0
Kowai River	573	93.7	36.1	0.93	5.04	0.48	140	8.5	8.9	7.4	66	11.4	0
Lower Farm Stream	547	131.6	5.9	0.50	2.82	0.37	53	6.9	8.7	7.4	68	12.5	0
Manson Creek	739	117.6	4.8	0.39	2.25	0.39	80	6.1	6.5	7.3	49	13.0	30
McNulty Stream[1]	899	126.9	3.2	0.33	2.21	0.33	119	4.7	5.0	7.5	50	12.0	0
Pass Stream[1]	865	116.3	2.8	0.29	2.64	0.34	68	7.0	6.6	7.3	51	11.5	20
Peacock Stream[1]	562	133.1	2.3	0.16	1.28	0.34	85	6.4	6.4	7.5	74	12.0	90
Slip Spring[1]	746	120.2	8.7	0.62	3.54	0.33	71	8.1	7.6	7.3	68	10.8	5
Waimak Spring[1]	480	127.9	1.4	0.72	5.23	0.34	51	8.6	8.8	6.8	68	10.7	0
Whitewater Stream	723	119.3	22.4	0.99	4.48	0.45	225	7.1	7.3	7.4	56	11.4	0

[1]Unofficial name.



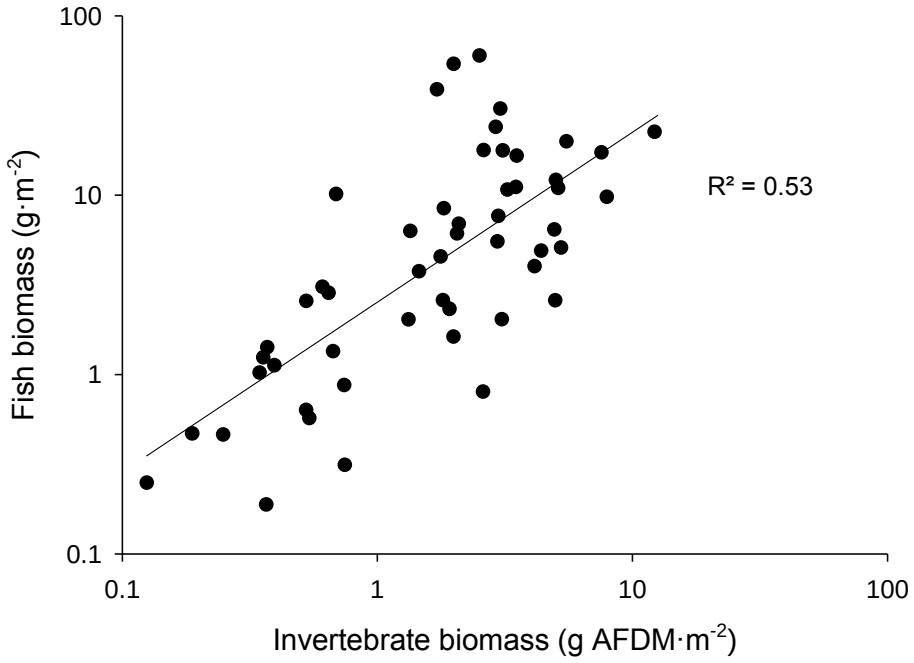
Appendix 2. The relationship between the frequency and intensity of disturbance at the 20 sites used in the intensive fish surveys for four different disturbance intensity cutoffs (20, 40, 60, 80% of bed moved, respectively). Mean tracer particle movement over the survey period was used as the intensity of disturbance index at each site. Frequency of disturbance was measured as the proportion of seven periods when the percentage of particles that had moved exceeded 20, 40, 60 or 80%, respectively.



Appendix 3. The relationship between disturbance and variation in fish biomass during the intensive fish surveys. The coefficient of variation (CV) for each data point (i.e., stream) is an average value for the five intensive surveys at each of the 20 streams.

Appendix 4. Correlation coefficients between the first two dimensions of non-metric multidimensional scaling (NMDS), representing the structure of stream fish communities and the contribution of the six most common fish species to total community biomass. Significance values are: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	NMDS axis 1	NMDS axis 2
Fish biomass		
Total	+0.39	+0.76***
Longfin eel	+0.23	+0.55*
Brown trout	+0.79***	+0.38
Rainbow trout	–0.72***	+0.34
Canterbury galaxias	+0.05	–0.23
Alpine galaxias	–0.23	–0.45*
Upland bully	+0.23	–0.04



Appendix 5. The relationship between invertebrate biomass (ash-free dry mass) and fish biomass (wet weight) at the 52 sites for the extensive survey.

Plate 3. Alpine galaxiids (*Galaxias paucispondylus*) are commonly found in flood-prone streams (Photo credit: Angus McIntosh).

Chapter Three

Disturbance-mediated prey assemblages determine fish community structure

Abstract

Disturbance is a strong structuring force that can influence the strength of species interactions at all trophic levels. Biotic interactions are predicted to change across gradients of environmental variability. However, how the contributions to community structure of top-down and bottom-up processes vary across gradients is poorly understood. In stream ecology, many studies have found top-down control to be important, but this may be because most experimental studies have been conducted in stable systems. I used surveys and experiments to assess whether fish communities were affected by the composition of their prey, and whether disturbance through direct effects on prey, indirectly influenced fish assemblages. The composition of prey communities was strongly related to disturbance, with the proportion of protected primary consumers (i.e., those with morphological defences) decreasing with increasing disturbance. Surveys indicated that fish species had different disturbance niches (i.e., their biomass peaked at different levels of disturbance), and results from a mesocosm experiment showed that fishes fed most efficiently on the prey species associated with their particular niche. An *in situ* experiment evaluating whether disturbance and/or prey assemblages influenced fishes indicated that predatory fish impacts on invertebrates declined with increasing disturbance and were more severe on unprotected than protected consumers. Disturbance did not affect fishes directly but affected prey community composition, which directly influenced fish weight. Collectively, my results showed that the importance of top-down processes on food webs weakened with increasing disturbance, but that disturbance-

mediated prey community composition resulted in bottom-up influences on fish community composition across a gradient of disturbance.

Introduction

Disturbance (i.e., environmental harshness) is a strong force structuring food webs because it can influence the strength of species interactions at all trophic levels (Sousa 1984, Pickett & White 1985, Wootton 1998). Some models of community regulation suggest that biotic interactions within and between trophic levels will only be important at low to moderate levels of environmental disturbance (Menge 1976, Peckarsky 1983, Menge & Sutherland 1987), although exceptions do occur (e.g., Thomson et al. 2002). Under relatively benign conditions, consumer-resource interactions at all trophic levels can be structured by both bottom-up (i.e., resource availability) and top-down (i.e., predation) processes (e.g., Dyer et al. 2003, Nyström et al. 2003), although the conditions under which each process dominates are still poorly understood (Meserve et al. 2003). Whilst the role of biotic interactions in disturbed environments is predicted to be weak, interaction strength in such habitats has rarely been quantified.

Whether top-down or bottom-up processes structure a food web will partly depend on the efficiency of prey consumption by predators (Power 1992a). Predation efficiency can be reduced through mechanisms such as predator abundance, inter- and intra-specific competition between predators, prey defences (morphological, behavioural or chemical) and increased refugia for prey (Power 1992a). All of these mechanisms can potentially determine the importance of top-down processes in structuring food webs, but they can also all be modified by disturbance (defined as "any relatively discrete event in time that removes organisms and opens up space which can be colonized by individuals of the same or different

species", Townsend 1989). The frequency of extreme climatic events (e.g., droughts, floods, storms) that bring about disturbance is predicted to increase under global climate change scenarios (IPCC 2001), so understanding how food-web structure and community dynamics change along gradients of disturbance is relevant to a wide range of ecological systems.

Disturbance is likely to have important direct and indirect effects on food-web structure and on predators in particular (Wootton et al. 1996). An increase in disturbance can reduce abundance of organisms at basal and consumer trophic levels through physical or physiological stress, thereby altering community structure and composition (Kennen et al. 2010). In contrast, species trait variation within a community can be considered to be an indirect effect of disturbance because species become adapted to exploit food resources under a particular set of environmental conditions. Individuals face a trade-off between traits for resistance/resilience to disturbance (e.g., high mobility, fast growth rates) and those that confer resistance to biotic interactions under more benign conditions (e.g., morphological defences) (Werner & Anholt 1993, Power et al. 1996, Wellborn et al. 1996, Grime 2001). However, traits that reduce vulnerability to predation or competition often increase the susceptibility of a species to disturbance (Wellborn et al. 1996, Wootton et al. 1996, Greig & Wissinger 2010). In fluvial ecosystems, protected consumers that invest energy in morphological defences (such as cases or shells) to reduce predation often have limited mobility and can be vulnerable in disturbed environments due to mortality from crushing when substrates move during floods (Otto & Svensson 1980). Such trait trade-offs are likely to result in a range of community structure along flood disturbance gradients (Death 2010).

In addition to species traits, prey availability to animals at higher trophic levels can be a strong determinant of community structure. For example, in stream ecosystems, predatory fishes may need to consume very large proportions of prey production to support their own production (Allen 1951, Huryn 1998). Whilst prey availability may limit predatory fish

abundance, the composition of prey assemblages may also have important implications for predatory fish community organisation, especially if a large proportion of the prey is protected/inedible (McCarter 1986). Protected prey such as Gastropods and many Trichopteran species produce heavy cases (relative to their body weight) which causes them to be largely restricted to the river bottom and therefore less abundant in invertebrate drift samples (Otto 1976). This has important implications for growth of drift feeding fishes such as salmonids, because it is usually more "energetically expensive" to forage on the river bed for prey items than to forage on drifting prey (but see Fausch et al. 1997). Most studies that have investigated the effects of fish on invertebrate communities (i.e., top-down fish predation and the role of fish in trophic cascades) have been conducted under stable conditions (e.g., Power 1990, Wootton et al. 1996). Therefore, our understanding of the relative importance of top-down and bottom-up processes is limited in scope, as few studies have assessed how these processes interact across the various disturbance gradients that characterise many lotic ecosystems.

I used a combination of surveys, mesocosm and *in situ* experiments to evaluate the effects of disturbance on prey and predator communities and to assess both bottom-up and top-down influences on community structure across a gradient of disturbance. First, I conducted surveys of predatory fish assemblages to determine how common fish species were affected by disturbance. I expected that the biomass of different predatory fish species (e.g., eels, galaxiids, trout) would peak at different levels of disturbance due to variations in their environmental tolerance, competitive ability and prey preferences (i.e., niche theory, Gause 1934). Second, I measured prey communities (i.e., invertebrates) to assess how the relative abundance of prey with particular traits (i.e., protected and unprotected consumers) varied with stream disturbance. I hypothesised that protected consumer biomass would be most abundant at stable sites, but would decline rapidly with increasing disturbance compared to

unprotected consumer biomass. Finally, experiments were conducted to test whether disturbance could influence predatory fish composition via its effect on prey communities, and whether predatory fish impact on invertebrates (i.e., top-down control) weakened with increasing disturbance.

Methods

Study Area

The influence of disturbance on stream invertebrate and fish communities was assessed from 2005 – 2009 at 74 sites in Canterbury and Westland, two contrasting regions of the South Island, New Zealand (Fig. 1). Westland has high rainfall (often > 4600 $mm \cdot yr^{-1}$) due to prevailing westerly winds and its proximity to the Southern Alps (that rapidly rise to 3000 m just 20 km inland). This high rainfall leads to high-gradient, flood-prone streams that drain the snowfields of the Alps, and also low-gradient streams that flow through podocarp-dominated, coastal rainforests. On the eastern slopes of the Southern Alps, rainfall and vegetation change dramatically. Rainfall in the Canterbury hill country rarely exceeds 1500 $mm \cdot yr^{-1}$ (decreasing with distance east) and vegetation is dominated by beech forest (*Nothofagus* sp.) and tussock grasslands.

Study sites were selected in these two regions (based on prior knowledge) to span a gradient of disturbance (achieved by having sites with contrasting flow regimes e.g., springs, braided rivers, etc.) and encompass a large range in stream size (width: 0.8 – 13.9 m, stream order: 2 – 5). Sites were sampled from September (early spring) through to April (mid-autumn) to avoid periods of low biological activity during winter. Fewer sites were sampled in Westland due to logistical constraints. At each site, a single-thread 50 m survey reach was

selected which was wadeable and less than 15 m wide (so it could be quantitatively electrofished). Within each reach, there needed to be a 25 m section containing at least one pool, run and riffle habitat for electrofishing. Sites were excluded if they: did not meet these criteria, were fishless, had pH values that may prohibit some fish species from being present (< 6 or > 8.5) or had high conductivity values (> 150 $\mu S \cdot cm^{-1}$; indicative of potential water pollution in these particular catchments).

Stream habitat and community sampling

Stream reach and channel stability, which reflect stream disturbance regimes, were assessed using the river disturbance index (hereafter abbreviated to RDI) (Pfankuch 1975). This index estimates disturbance due to flooding based on 15 categories that evaluate landscape, riparian and stream characteristics. The observer visually grades each category and the scores are summed to give an overall index score (RDI range: 38–152). Low scores indicate the waterway is stable, whereas physically unstable/highly disturbed waterways have higher scores. Previous studies have shown that the RDI strongly correlates with measures of stream bed movement (e.g., Death & Winterbourn 1994, Townsend et al. 1997b, Greenwood & McIntosh 2008), and my research (Chapter 2) indicates that the index is highly correlated with substrate movement across a much broader disturbance gradient (RDI scores: 57-141).

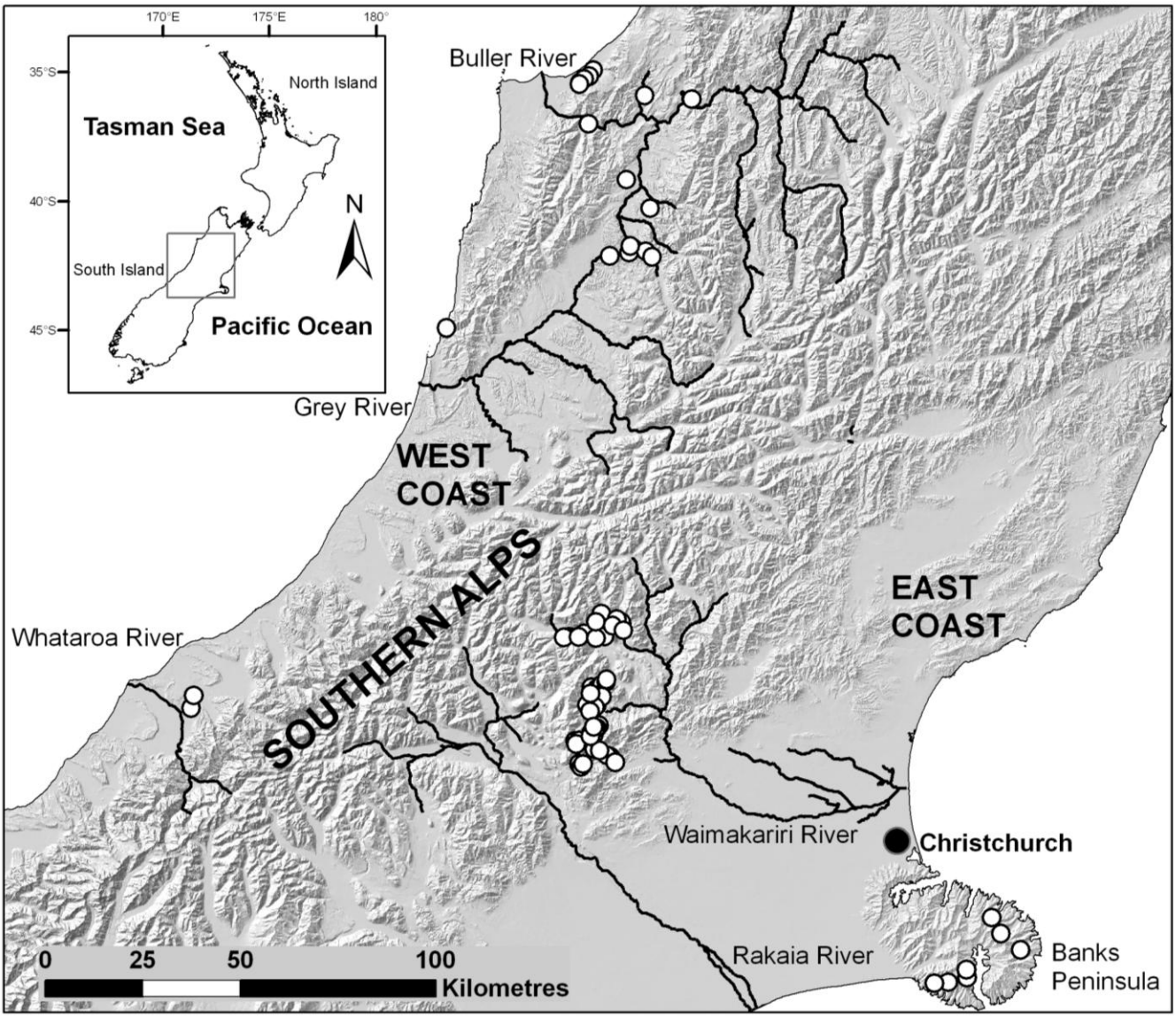


Figure 1. The location of survey sites (white circles) on the western and eastern sides of the Southern Alps, South Island, New Zealand. Only selected major rivers are identified.

Stream communities in both grassland and forested catchments were sampled from April 2005 to May 2009. Winter sampling was avoided during this four-year period to ensure communities were not being sampled during times of low biological activity. Invertebrate samples were taken at 69 sites to determine how prey resources for predatory fish varied spatially and temporally with disturbance. Five Surber samples (0.0625 m², 250 µm mesh) were taken within a 50 m stream reach to determine aquatic invertebrate abundance. One sample was taken every 10 m in riffle or run habitat. Invertebrates were preserved in 90%

ethanol, and sorted and identified in the laboratory at a magnification of ×10. Aquatic invertebrates were identified to either genus or species level (except Chironomidae, which were identified to sub-family) using the keys of Winterbourn et al. (2000) then sorted into five groups for weighing and ashing: mayflies, predatory invertebrates, dipterans, cased consumers and other aquatic invertebrates. Ash-free dry mass (AFDM) of each group was calculated by air drying for at least 48 h at 50 °C, followed by ashing at 550 °C for 4 h. At each stage of the drying and ashing process, samples were weighed to the nearest 0.1 mg on a Mettler Toledo AB204-S balance (Küsnacht, Switzerland). AFDM of cased and shelled consumers (i.e., Gastropods and many Trichopteran species) was used to calculate the biomass of protected consumers, and the AFDM of the other four groups (including predatory invertebrates, which are known to be consumed by fish) was combined to calculate unprotected consumer biomass.

To investigate how fish communities varied with disturbance across space and time, at least 25 m (but up to 50 m) of river was quantitatively three-pass electrofished with stop nets at 74 sites (five additional sites were sampled where invertebrate communities were not measured). All streams were surveyed using a Kainga EFM 300 backpack electrofishing machine (NIWA Instrument Systems, Christchurch, N.Z.) with 300 – 600 V pulsed DC (pulse width ~ 3 ms, 60 pulses s^{-1}), with the operator moving in a downstream direction towards a 1 m wide push net (mesh size 3 × 2 mm ellipse). Electrofishing in a downstream direction is the most efficient method for capturing fish species in these streams (Jellyman & McIntosh 2010). All captured fishes were anaesthetized with 2-phenoxyethanol, measured [to the nearest 1 mm; fork length (FL) for salmonids and total length (TL) for other species], weighed and released. Fish densities were calculated using the maximum likelihood equations for three-pass depletion sampling (Cowx 1983).

Drift sampling

The relationship between the abundance of drifting invertebrates and stream fish communities was investigated by surveying 15 sites in the upper Waimakariri River catchment (4 – 7 April 2005). Selected sites were spread across gradients of stream size (width: 0.9 – 13.5 m) and disturbance (RDI scores: 65 – 140). The fifteen sites were pre-selected so that a balance between trout- and galaxiid-dominated fish communities was achieved (5 trout only, 5 galaxiid only, 5 with both). Ten of the sites had eels present. Two drift nets (30 × 25 cm front opening, 1 m long, 200 µm mesh) were placed in riffles at each site for approximately two hours during the day (starting 0930 hours) and night (starting 2100 hours). Four sites were sampled each day, and nets were placed in the same location for day and night sampling. Water velocity through the drift nets was measured using a current meter (Marsh-McBirney Flo-Mate® Model 2000, Frederick, MD, U.S.A.) at the start and finish of drift sampling to calculate the volume of water each net had filtered. The benthic density of invertebrates at each site was estimated by sampling six cobbles [principal axis (pa): 100 – 220 mm] prior to drift sampling. Cobbles were randomly selected downstream of the area where the drift nets would be installed, and individual cobbles were sampled by first placing a net (250 µm mesh) underneath each rock then washing off the invertebrates inside the net. The surface area of the each cobble was then measured and the invertebrates pooled. Invertebrates from drift nets and benthic sampling were preserved in 90% ethanol, and processed, weighed and ashed as described above. Drift density was calculated using Equation 1 of Allan & Russek (1985) and expressed as numbers m^{-3} of water filtered. In analyses, drift propensity (measured as: drift density/benthic density) was used as the response variable to account for differences in drift due to variations in benthic density.

Mesocosm predation experiment

The predatory ability of three fish species (*Salmo trutta*, *Galaxias vulgaris* and *Anguilla dieffenbachii*) was investigated by manipulating prey community composition in mesocosm experiments. Consumption of two prey communities, composed of either protected taxa (cased-caddisflies: *Pycnocentrodes* sp. and *Pycnocentria* sp.) characteristic of stable streams or unprotected taxa (mayfly: *Deleatidium* spp. and stonefly: *Zelandoperla* sp.) representative of disturbed streams, was compared[2]. The experiment had eight treatment combinations (3 fish sp. + no predator control × prey type), each with four replicates. Sixteen oval black polythene tanks (1.21 × 0.68 m, 0.82 m²) at the University of Canterbury's Cass Field Station (see Plate 4) were used in two experimental runs (March 13 – 15 and March 29 – 31, 2008). Each tank was supplied with water pumped from Grasmere stream (pH, 7.4; conductivity, 104 μS_{25} cm^{-1}; dissolved oxygen, 10.6 – 11.2 mgL^{-1}) at a rate of 0.1 L s^{-1}, screened to remove invertebrates and debris. Water temperature was recorded hourly using WT-HR loggers (Trutrak, Christchurch, N.Z) and indicated there was no significant difference in mean water temperature (paired *t*-test, $P > 0.05$) between experimental runs (Run 1: mean 13.7 °C, range 12.6 – 15.6 °C, Run 2: mean 14.1 °C, range 12.5 – 15.1 °C). A central standpipe with openings covered by 2 mm mesh regulated water depth in each tank at 22 cm and stopped prey from escaping. Two perspex baffles (28 × 35 cm) were attached to the standpipe to direct water from two jets on opposite sides of the tank, producing circular flow (Plate 4). Water velocity within each tank ranged from 0.03 – 0.21 m s^{-1} depending on proximity to the water jets, and was similar between tanks. Tank bottoms were covered with a layer of dry, cleaned gravel particles (pa: 10 – 50 mm) sourced from the nearby Cass River. Ten periphyton-covered large cobbles (pa: 130 – 200 mm) were placed in each tank to provide food for grazing invertebrates and cover for fish (see Plate 4). The cobbles were sourced from the

[2] Consumption was not directly measured, but rather assumed to be equivalent to the reduction in prey items during the experiment.

Plate 4. Array of 16 tanks at the Cass field station used in the mesocosm predation experiment (top) and the 10 algal-coated cobbles that were placed in each tank prior to the introduction of biota (bottom). The direction of water jets (large arrows), together with the baffles and standpipe produced circular flow. Tanks were covered by 1 mm mesh to prevent terrestrial insects and birds from entering the tanks, and to stop fish from escaping (see top photo).

same river for both experimental trials and had comparable algal biofilm cover on both occasions. For both experimental runs, caddisflies were collected from a stable spring tributary of the Waimakariri River (One Tree Swamp Spring), and mayflies and stoneflies from the disturbed mainstem of the Waimakariri River, near Cass. Both waterways had galaxiid, trout and eel species present, so invertebrate behavioural responses would not be affected by unknown predatory fish cues (see McIntosh et al. 1999). Four hundred prey taxa of similar length (*c.* 10 mm) were added to each tank at densities representative of particular stream types (i.e., stable treatments: 350 *Pycnocentrodes* sp., 50 *Pycnocentria* sp.; disturbed treatments: 395 *Deleatidium* sp., 5 *Zelandoperla* sp.). At the conclusion of each experimental run, all cobbles and gravels were rinsed through a series of sieves to collect invertebrates, which were preserved in 90% ethanol. In the laboratory, prey were counted, weighed and ashed (see above).

Fish were sourced from two tributaries of the Waimakariri River (Roadmarker Stream and Cave Stream). Both tributaries contained all three fish species, and all four prey species. One fish was introduced into 12 of the 16 tanks for each experimental run (the remaining four tanks were fishless controls). The weight of fish used in the experiment was kept constant (16 – 19 g) by varying the length of the different species used (*S. trutta*: 107–114 mm; *G. vulgaris*: 115 – 125 mm). However, because *A. dieffenbachii* shifts from living within substrates to open water at sizes greater than 300 mm (Jellyman et al. 2002) all eels used in the experiment needed to be > 300 mm to ensure they would be consuming open water prey species. Eels were therefore larger and heavier than the other fishes used (length: 310 – 317 mm, weight: 58 – 62 g). Only one fish was placed in each tank to keep fish density and biomass within a realistic range of observed field values. Balancing the trout and galaxiid biomass and fish density within the tanks provided a constant predator density for analysis. Eels were not tested in the second experimental run because they consumed very few prey

during the first run. They were replaced with another galaxiid and trout replicate for each prey type on the second run.

In situ *predation experiment*

To assess how prey assemblage influenced the condition of predatory fishes, the same three fish species used in the prey consumption experiment (*S. trutta*, *G. vulgaris* and *A. dieffenbachii*) were tested in an *in situ* experiment. The experiment used 36 cages (Fig. 2), which were left in streams varying in degree of disturbance for 40 days. Three cages were placed into 12 streams that spanned the disturbance gradient (RDI range: 54 – 141), with one fish placed in each cage (i.e., one trout, galaxiid and eel was caged at each site). Cages were spaced at least 15 m apart and held in place by four steel posts. Twenty litres of dry, cleaned gravel was placed on the cage bottom to create consistent riverbed conditions in each cage. Ten cleaned cobbles (pa: 100 – 200 mm) were placed on top of the gravel layer and then left to be colonised by algae to act as a resource (i.e., food/habitat) for invertebrates and fish. The stainless steel mesh on the front and back of each cage was kept as large as possible (6.5 mm mesh) to allow as many invertebrates as possible to enter and reduce screen clogging whilst still containing all fish species. The smaller (2 mm mesh) plastic mesh on the top of the tanks excluded aquatic and terrestrial invertebrates from entering the cages from above but still allowed light to penetrate through to the cobbles in the cages for algal growth.

Cages were put in rivers on 7 – 8 January 2009 and were left to be colonised by algae and invertebrates for 18 days (mesh was cleaned every two or three days so that invertebrate access to the cages was not impaired). During this colonisation period, all 12 sites were quantitatively electrofished to determine whether fish density and biomass was within the expected range for the level of disturbance (i.e., streams were in a ‘typical’ state when the fish

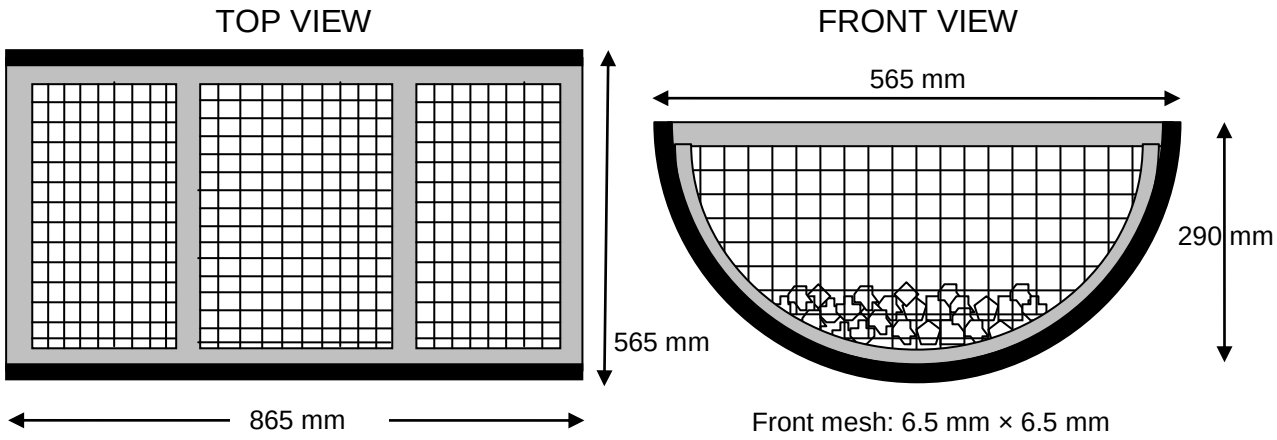


Figure 2. Dimensions of the cages used for the *in situ* predation experiment. Hatching denotes areas of mesh, wooden framing is coloured grey and solid black areas represent black plastic. The cages had an internal volume of 125 litres (Suren & Lambert 2006). The height of the gravel relative to the cage front is also shown.

were put into cages). Two cobbles from within each cage were sampled for invertebrates immediately prior to fish introduction to the cage. A comparison between cage cobble and stream benthic Surber samples (25 cm × 25 cm) showed that invertebrate biomass in the cages was not significantly different from that in the streams at the start of the experiment (nested ANOVA: $P > 0.3$).

Fish were placed in cages on 22 – 23 January 2009 and left there for 22 days (i.e., until 12 – 13 February 2009). Fish used were sourced from Roadmarker Stream and Cave Stream; see above). Each fish was measured (nearest 0.5 mm) and weighed (nearest 0.1 g) at 0, 7 and 22 days. Weight change was the main fish response variable, so fish were weighed three times immediately after each (and averaged) to account for any surface water on the fishes that may have affected the weight measurements (although repeated measures did not vary by more than 0.1 g). So results would be comparable, the length and weight of each fish species was kept similar to those used in the mesocosm predation experiment (i.e., 16 – 22 g; *S. trutta*: 111 – 123 mm, *G. vulgaris*: 124 – 133 mm). Trout and galaxiids were also paired by weight at each site so that the starting weight difference between the two taxa was less than

2.5 g. Eels were difficult to obtain in the narrow size range required for the prey consumption experiment, and more than 100 were captured in an attempt to obtain experimental individuals of a standard size. Even so, the 12 selected eels ranged in size from 302 to 346 mm (55 – 77 g).

Invertebrate drift was sampled midway through the *in situ* predation experiment (29 – 30 January 2009) using the same methods outlined in the "drift sampling" section (above) to estimate invertebrate biomass (aquatic and terrestrial) entering the cages. Day drift was sampled between 1030 and 1700 h for 150 – 180 minutes with nets installed 1 m upstream of each cage (Plate 5). A Surber sample was taken alongside the drift net to calculate benthic invertebrate density and biomass at the time of drift sampling.

At the conclusion of the experiment, a Surber sample was taken in close proximity to each cage (i.e., 3 Surber samples per stream) to assess whether stream invertebrate communities had significantly changed over the 22 day experimental period. This was done because not enough cages were available to install a control cage (i.e., no fish) at each site to assess how invertebrate communities responded in the absence of a fish predator. To sample cage invertebrate communities, the cages were lifted onto the stream bank where the cobbles and gravel were rinsed through a series of sieves to collect invertebrates. The invertebrates from all drift, Surber and cage samples were identified to either genus or species level (except Chironomidae which were identified to sub-family) using the keys of Winterbourn et al. (2000). Each invertebrate sample was then sorted into five groups for weighing and ashing (for methods see stream sampling section): mayflies, predatory invertebrates, dipterans, cased consumers and other aquatic invertebrates. Drift samples had two extra groups: adult aquatic insects and terrestrial insects.

Plate 5. Images of the *in situ* predation experiment, clockwise from top left; cages at a stable stream (Slip Spring), where an extra steel post was installed upstream to reduce mesh clogging by macrophytes; a cage installed in a large, disturbed stream (Cass River); drift nets installed to sample invertebrates entering a cage; all three cages installed in Bruce River.

Water height, water temperature and air temperature were recorded hourly at all sites using WT-HR loggers (Trutrak, Christchurch, N.Z) from December 2008 to March 2009. During the experimental period, mesh screens were cleaned every two to three days. Some cages became moderately clogged (*c.* 50% flow reduction through cages), whilst other cages did not clog at all (< 5% flow reduction). Water velocity was measured at the front and back of each cage prior to cleaning so that flow reduction into the cages (and therefore invertebrate drift) could be accounted for in analyses. On each screen cleaning occasion, water depth at the front of the cage was also measured so that the volume of water going through each cage could be calculated.

Data analyses

As the distribution of fish biomass was of particular interest in the stream surveys, relationships between disturbance and biomass for the five most common fish species were analysed using quantile regression splines from general additive models. Quantile regression splines can fit non-linear curves to data sets to define the upper or lower limits for a set proportion (i.e., 90^{th}, 95^{th} etc.) of a dependent variable's response to an independent variable. Therefore, this analysis illustrated the upper limits of population responses across the habitat gradient (Konrad et al. 2008). To be robust to outliers, the 90^{th} quantile was fitted to the data sets. Since fish biomass decreases with disturbance, the fitted biomass curves for the five fish species were normalised against the maximum fitted biomass (i.e., fitted biomass/maximum fitted biomass) to assess overlap in the 'disturbance niche' of each species. Relationships between disturbance, and invertebrate benthic and drift abundance were all fitted with non-linear regression (exponential decay curves).

Prey-assemblage and predator species effects on fish condition in the mesocosm experiment were tested using two-way analysis of variance (ANOVA) with tanks as replicates. Two analyses were conducted because the experimental design was unbalanced after eels were dropped from the second run. Significant differences (at $P < 0.05$) between treatment means were evaluated using Tukey's post-hoc comparisons. Linear regression analysis was used to investigate weight changes and size selectivity (as indicated by a non-random assemblage of uneaten prey sizes in the tanks) of the experimental fishes.

In the *in situ* predation experiment, the log-ratio of effect size (P) was used to quantify the impact of predatory fishes on prey biomass (Berlow 1999). Predator impact (P) = $\ln(Ba/Br)$, where Ba is total prey biomass in the caged predatory fish treatment and Br is total prey biomass in the ambient (i.e., stream) predatory fish treatment. All aquatic invertebrate species were considered prey and predator effect size was calculated for all consumers,

protected consumers and unprotected consumers. The effect of predatory fishes on prey communities (*P*) was initially assessed using homogeneity of slopes tests that included fish species as a covariate, the RDI as a continuous predictor, and the fish species by disturbance interaction. Response variables with a non-significant interaction term in the homogeneity of slopes tests were then analysed using ANCOVA with fish species and RDI as the main effects. The effects of fish species, unprotected consumers and disturbance on changes in fish weight were also tested using homogeneity of slopes tests and ANCOVA.

Results

The influence of disturbance on fish communities

Biomass of the five most common fish species peaked at different levels of flood disturbance (Fig. 3). Ninetieth quantile regression splines indicated *G. vulgaris* biomass peaked at stable sites and declined with increasing disturbance (Fig. 3). *A. dieffenbachii* had high biomass (≥ 15 $g \cdot m^{-2}$) at stable sites (i.e., RDI < 75), but its biomass quickly declined with increasing disturbance. *S. trutta* biomass peaked at intermediate disturbance scores of 75 (Fig. 3). The other trout species, *Oncorhynchus mykiss*, peaked at a similar disturbance score to *S. trutta* (albeit at a lower maximum biomass) but maintained higher biomass than *S. trutta* as sites became increasingly disturbed. Biomass of *G. paucispondylus* peaked at a much higher disturbance score (RDI = 102) than that of the other four fish species. The five species comparison of normalised biomass showed that whilst the biomass of four fish species peaked in relatively stable habitats (RDI < 80), only *G. paucispondylus* could maintain high biomass (relative to their peak) in highly disturbed streams.

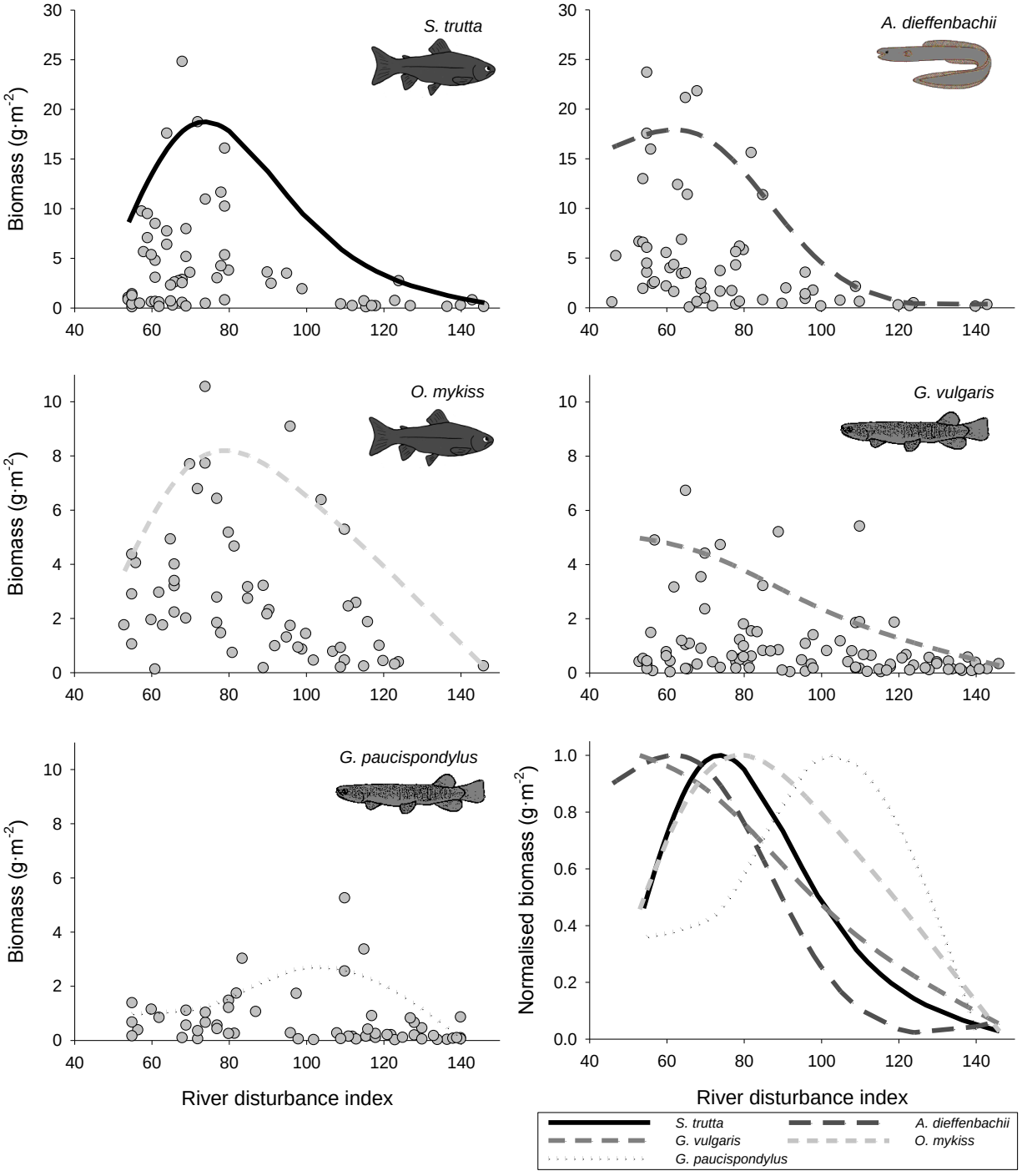


Figure 3. Biomass plotted against disturbance for the five most common fish species with quantile (90^{th}) regression splines fitted to show shifts in biomass peaks for each species. Normalised biomass curves for all species are plotted on the bottom right graph. Note the biomass scale is greater in the *S. trutta* and *A. dieffenbachii* graphs.

Disturbance effects on invertebrate communities

Biomass of both unprotected and protected invertebrate consumers declined significantly with increasing disturbance (Figs. 4a, b). At all 69 sites, the biomass of unprotected consumers was greater than that of protected consumers. Unprotected consumers had a twelve-fold decrease in biomass (4.1 to 0.26 g AFDM·m^{-2}) as disturbance increased (Fig. 4a), but protected consumer biomass declined at twice that rate (decreasing from 0.74 to 0.002 g AFDM·m^{-2}, Fig. 4b).

Unprotected and protected consumers differed in drift propensity. Drift propensity of unprotected consumers increased exponentially as sites became more disturbed (Fig. 4c), whereas drift propensity of protected consumers decreased with increasing disturbance. Few protected consumers were found drifting at sites with a disturbance score (RDI) greater than 70 (Fig. 4d). Fish biomass declined exponentially with increasing disturbance at the 15 drift sites (Fig. 4e). Therefore, fish biomass was inversely correlated with unprotected consumer drift propensity indicating that the relative drift of unprotected consumers was highest when disturbance was high and fish biomass was low. The effect of fishes on drift density was also tested. Total consumer drift density was significantly higher at sites without trout (one-way ANOVA: $F_{1,\ 13} = 15.84$, $P = 0.002$), and unprotected consumer drift density declined significantly with increasing trout biomass [$y = 59.2 - 19.0ln(x)$, $R^2 = 0.63$, $P = 0.01$]. No significant relationships between fish abundance and drifting invertebrates were identified for other fish species.

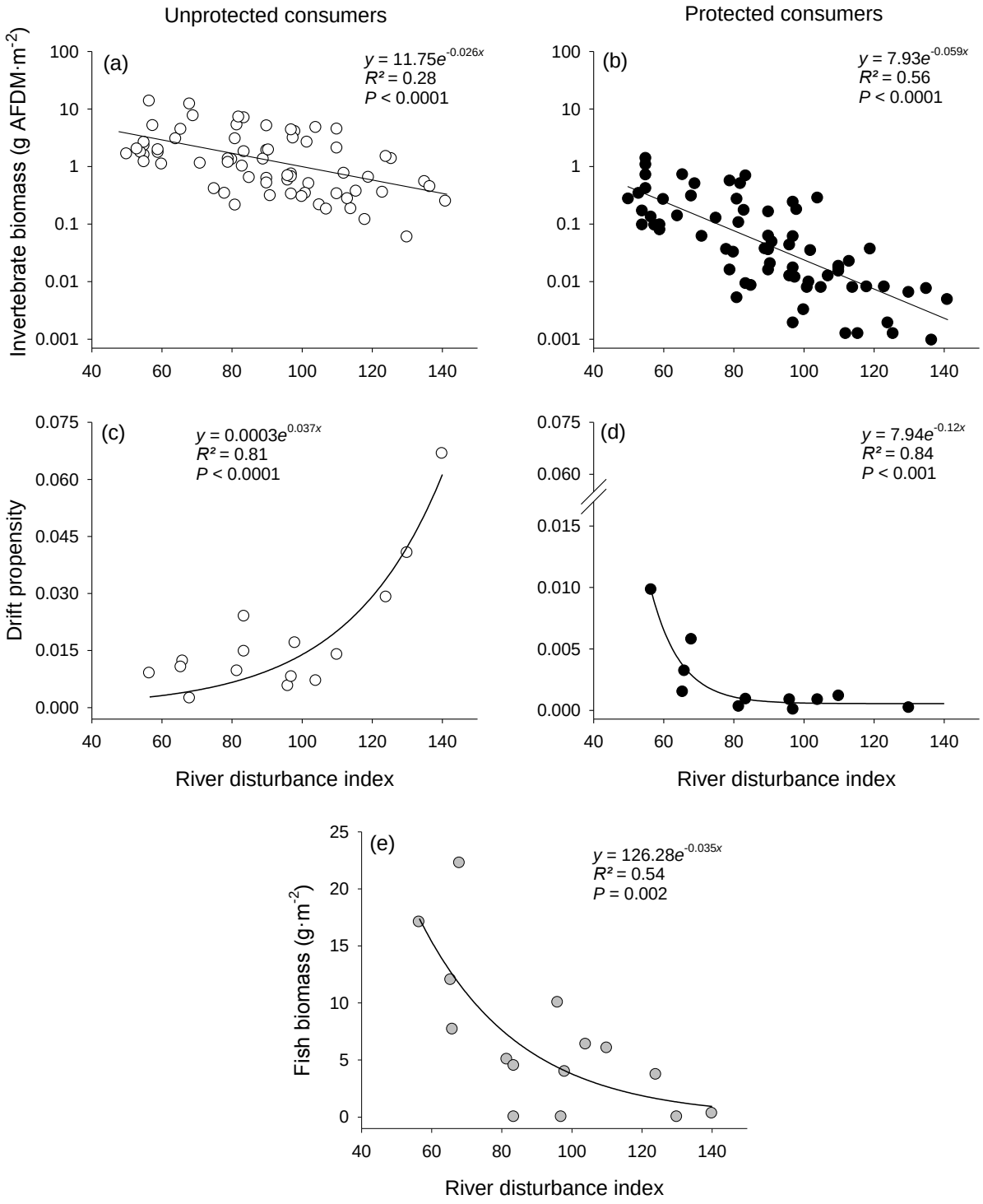


Figure 4. Relationships between disturbance (RDI) and biomass of (a) unprotected consumers and (b) protected consumers at all sites, and (e) fish biomass at drift sampling sites. The change in drift propensity as disturbance increased is shown for (c) unprotected consumers and (d) protected consumers at 15 sites (protected consumers were only present in the drift at 11 sites).

Mesocosm predation experiment

A significant interaction between prey type and fish species (in both experimental runs) indicated that the percentage of prey consumed was affected by the type of prey being eaten and the fish species feeding on it (Table 1). On average eels consumed 2% of the protected prey and 5% of the unprotected prey, although predation rates were not significantly different from prey losses in fishless controls (Fig. 5a). Prey types were consumed in similar proportions by galaxiids with 10% and 9% of the protected and unprotected prey eaten, respectively (Fig. 5a). Galaxiids consumed significantly more protected prey than eels but not significantly more unprotected prey. Mean protected prey consumption by trout was 18%, but this predation rate was not significantly different from the galaxiid rate (Fig. 5a). Trout consumed 46% of unprotected prey which was significantly more than their predation of protected prey. Trout predation of unprotected prey was also significantly greater than the consumption of either prey type by eels and galaxiids (Fig. 5a).

For protected prey, the relationship between the average weight of prey remaining (following fish predation) and the percentage of prey consumed had a *y*-intercept of 51% (Fig. 5b), whereas the *y*-intercept was 90% for unprotected prey (Fig. 5b). The weight of remaining prey is zero grams when prey consumption is 100%, and a *y*-intercept close to this value suggests random predation of prey items by fishes. Therefore, the *y*-intercept of 51% for protected consumers is indicative of strong size-selectivity by all fish species on protected consumers but random prey selection of unprotected consumers.

The body weight of trout decreased when they consumed protected prey but generally increased when consuming unprotected prey (Fig. 5c). A significant linear relationship was found between the percentage of prey consumed and trout weight change, and indicated that trout weight increased with increasing predation (Fig. 5c). A similar linear relationship was

not found for galaxiid fishes, indicating that galaxiid weight changes did not differ significantly with prey type (one-way ANOVA: $F_{1, 9} = 2.23$, $P = 0.17$).

Table 1. Two-way ANOVA testing the effects of prey type and fish species on the percentage of prey eaten during each run of the prey-assemblage predation experiment.

Variable	*df*	*F*	*P*
Run 1			
Prey type	1	32.47	**0.0004**
Fish species	3	57.55	**< 0.0001**
Prey type × Fish species	3	10.06	**0.004**
Error	8		
Run 2			
Prey type	1	14.88	**0.003**
Fish species	2	55.66	**< 0.0001**
Prey type × Fish species	2	14.12	**0.001**
Error	10		

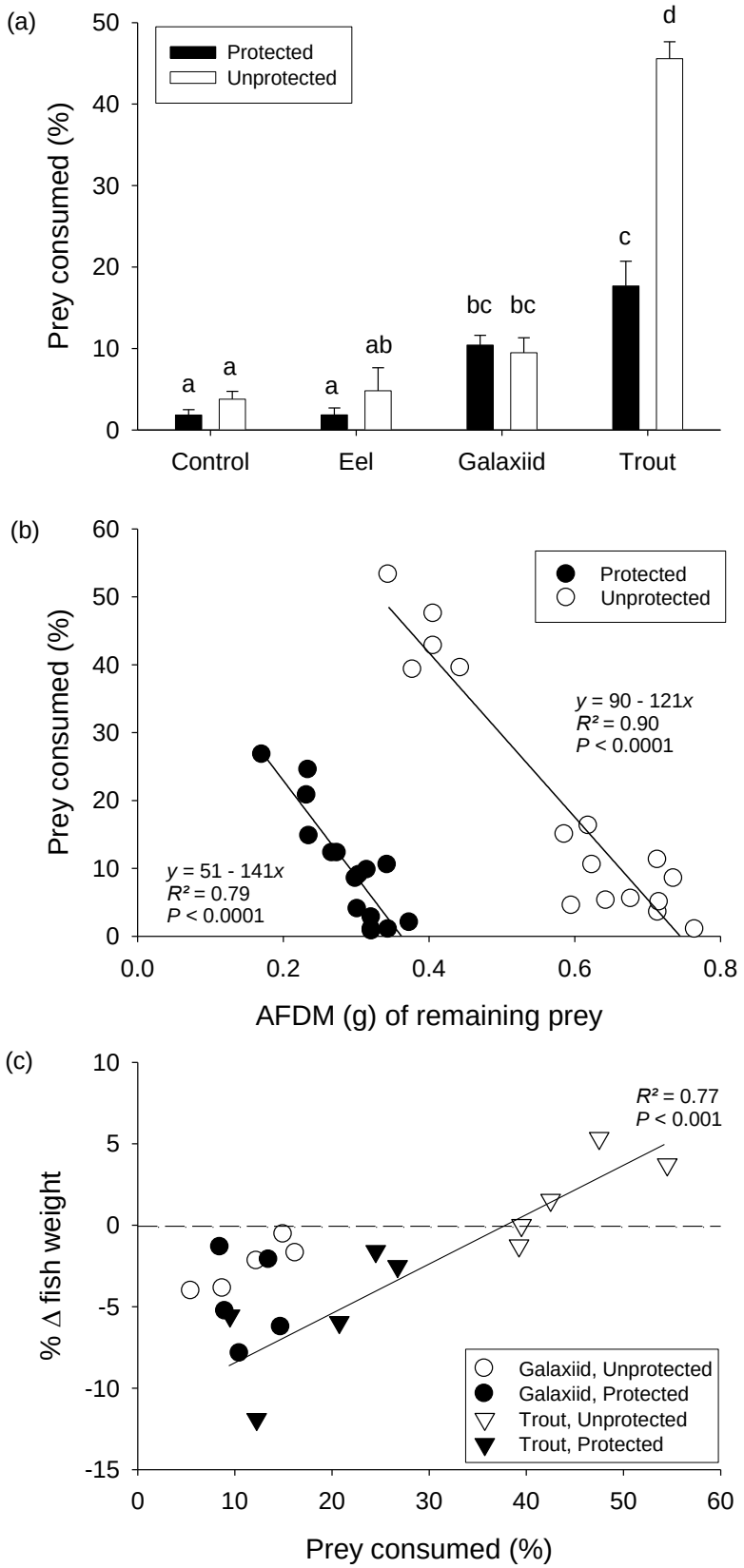


Figure 5. (a) Protected and unprotected prey consumption by each fish species. (b) The weight of each prey type consumed as a function of total prey consumption. (c) The relationship between total prey consumption and changes (% Δ) in galaxiid and trout weight. Lower case letters in (a) show significant differences ($P < 0.05$) indicated by Tukey tests.

In situ *predation experiment*

None of the physical variables measured (e.g., stage height, air and water temperature, average velocity, stream cross-sectional area) were significantly correlated with the river disturbance index (RDI) in the experiment. Significant negative relationships were found between fish biomass and disturbance (R^2 = 0.61, P < 0.001) and invertebrate biomass and disturbance (R^2 = 0.76, P < 0.0001) in the 12 experimental streams. Mean invertebrate biomass values at the start of the experiment ranged from 0.1 to 2.8 g AFDM·m^{-2} in the 12 streams.

Invertebrate biomass in the streams did not change significantly over the 22-day experiment (paired *t*-test: t = 0.69, df = 35, P = 0.49). However, the biomass of invertebrates in the cages was significantly correlated with the amount of drift entering them (see Appendix 1). Therefore, cages that received higher invertebrate drift had a higher biomass of benthic invertebrates. At the end of the experiment, the biomass of invertebrates in the cages was significantly lower than stream biomass (paired *t*-test: t = 2.51, df = 35, P = 0.02), so further analyses investigating the effect of disturbance and predatory fishes on cage invertebrate communities were conducted.

The impact of predatory fishes on invertebrate communities decreased as disturbance increased (Table 2a). For the three main prey community response variables measured (total, unprotected and protected consumer biomass), the slopes of the relationship between the predatory fish impact index and disturbance were not significantly different for the three fish species (Table 2a-c). However, predatory fishes had a significantly larger effect on unprotected consumers than protected consumers across the disturbance gradient (Table 2d), although regression lines were parallel so the change in impact across the disturbance gradient was identical for both consumer types (Fig. 6). Unprotected consumer biomass was affected

by predatory fishes at low and moderately disturbed sites (i.e., RDI scores ≤ 100), but predatory fishes only affected protected consumer biomass at the most stable sites (Fig. 6).

Table 2. Results of homogeneity of slopes tests and ANCOVA for the effect of fish species and disturbance on the predatory fish impact index. The index was used to assess impact on total consumer, unprotected consumer and protected consumer biomass. A fourth analysis was done using consumer type (unprotected or protected) as a main effect. In this latter analysis, the mean index for each site was used as a replicate because impact indices at each site (i.e., fish main effect) did not vary significantly in the other analyses. The significance level (*P*) of the *F*-test statistic is displayed in bold if $P < 0.05$.

Variable	*df**	*df*	*F*	*P*
a) Total consumers				
Fish		2, 32	1.04	0.37
Disturbance		1, 32	36.38	**< 0.0001**
Fish × Disturbance*	2, 30		0.04	0.96
b) Unprotected consumers				
Fish		2, 27	0.038	0.69
Disturbance		1, 27	17.18	**0.0003**
Fish × Disturbance*	2, 25		0.09	0.92
c) Protected consumers				
Fish		2, 32	1.12	0.34
Disturbance		1, 32	26.57	**< 0.0001**
Fish × Disturbance*	2, 30		0.08	0.92
d) Consumer type				
Consumer		1, 20	6.41	**0.02**
Disturbance		1, 20	20.14	**0.0002**
Consumer × Disturbance*	1, 19		0.02	0.90

* Obtained from homogeneity of slopes tests run prior to the model containing only main effects

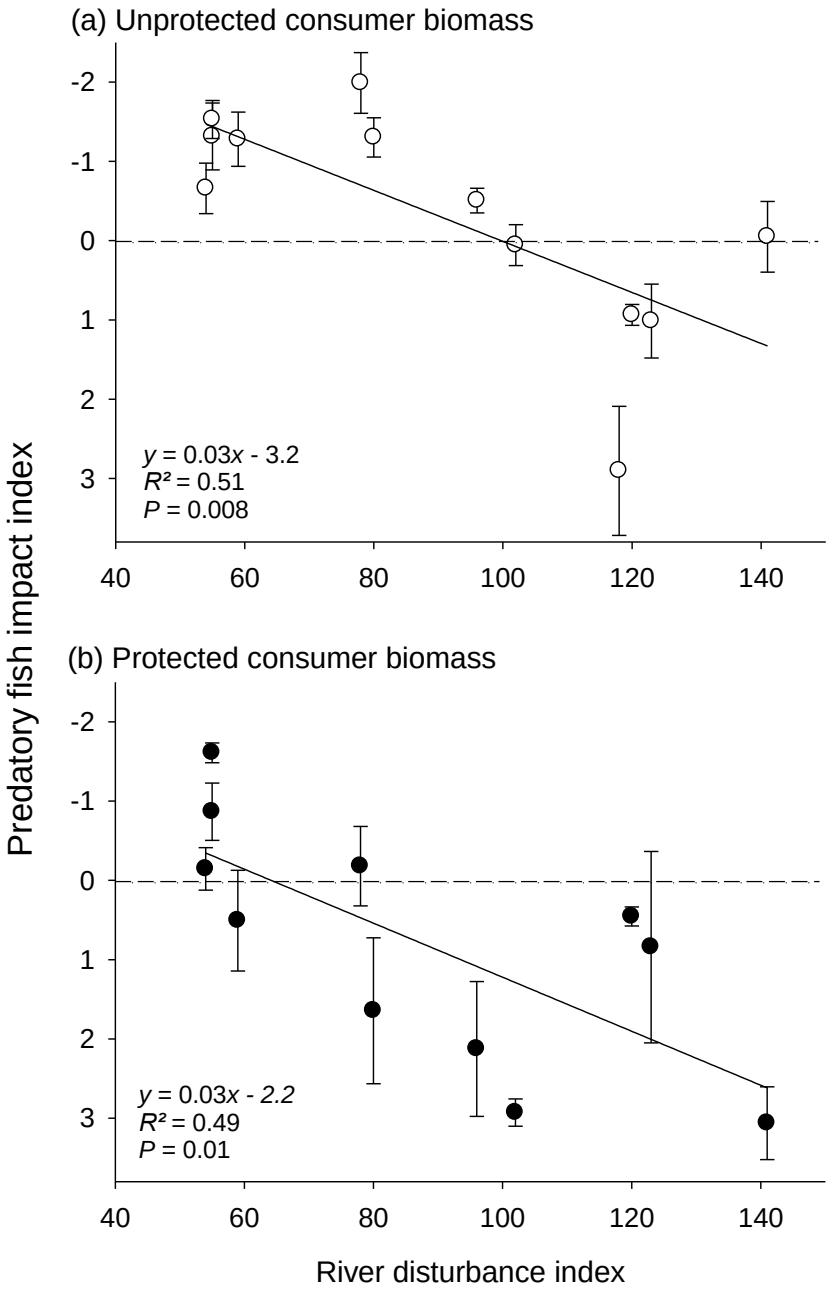


Figure 6. Changes in the predatory fish impact index across the disturbance gradient for (a) unprotected consumer biomass, and (b) protected consumer biomass. Negative values indicate a reduction of consumer biomass by predatory fish. Increasingly positive values indicate that the impact of predatory fish on consumer biomass is weaker. One site had no protected consumers throughout the experiment so graph (b) has 11 data points.

Over the three week experimental period, there was a significant effect of disturbance on fish weight (Table 3) with fish weight decreasing with increasing disturbance. However, fish species did not affect this relationship as the fish species × disturbance interaction was not significant (Table 3, Fig. 7). A significant fish species × proportion of unprotected consumers interaction (Table 3), and the results of linear regression analysis indicated quite different weight responses by each fish species to variation in unprotected consumer proportion during the *in situ* predation experiment (Fig. 7). As the proportion of unprotected consumers increased (in either the stream or the cage), eel weight declined, galaxiid weight did not change and trout weight increased (Fig. 7).

Table 3. Results of the homogeneity of slopes tests and ANCOVA (with 2 covariates) testing the effects of fish species, the proportion of unprotected consumers (in cages) and disturbance (RDI) on changes in fish weight. For simplicity, unprotected consumer data for cages were used, as changes in fish weight were very similar for cage and Surber sample data (see Fig. 7).

Variable	*df**	*df*	*F*	*P*
Fish		2, 29	8.57	0.001
Unprotected (cage)		1, 29	2.07	0.16
RDI		1, 29	7.81	0.009
Fish × Unprotected (cage)		2, 29	6.61	0.004
Fish × RDI	2, 27*		0.82	0.45
Fish × Unprotected (cage) x RDI	2, 24*		1.74	0.19

* Obtained from homogeneity of slopes tests

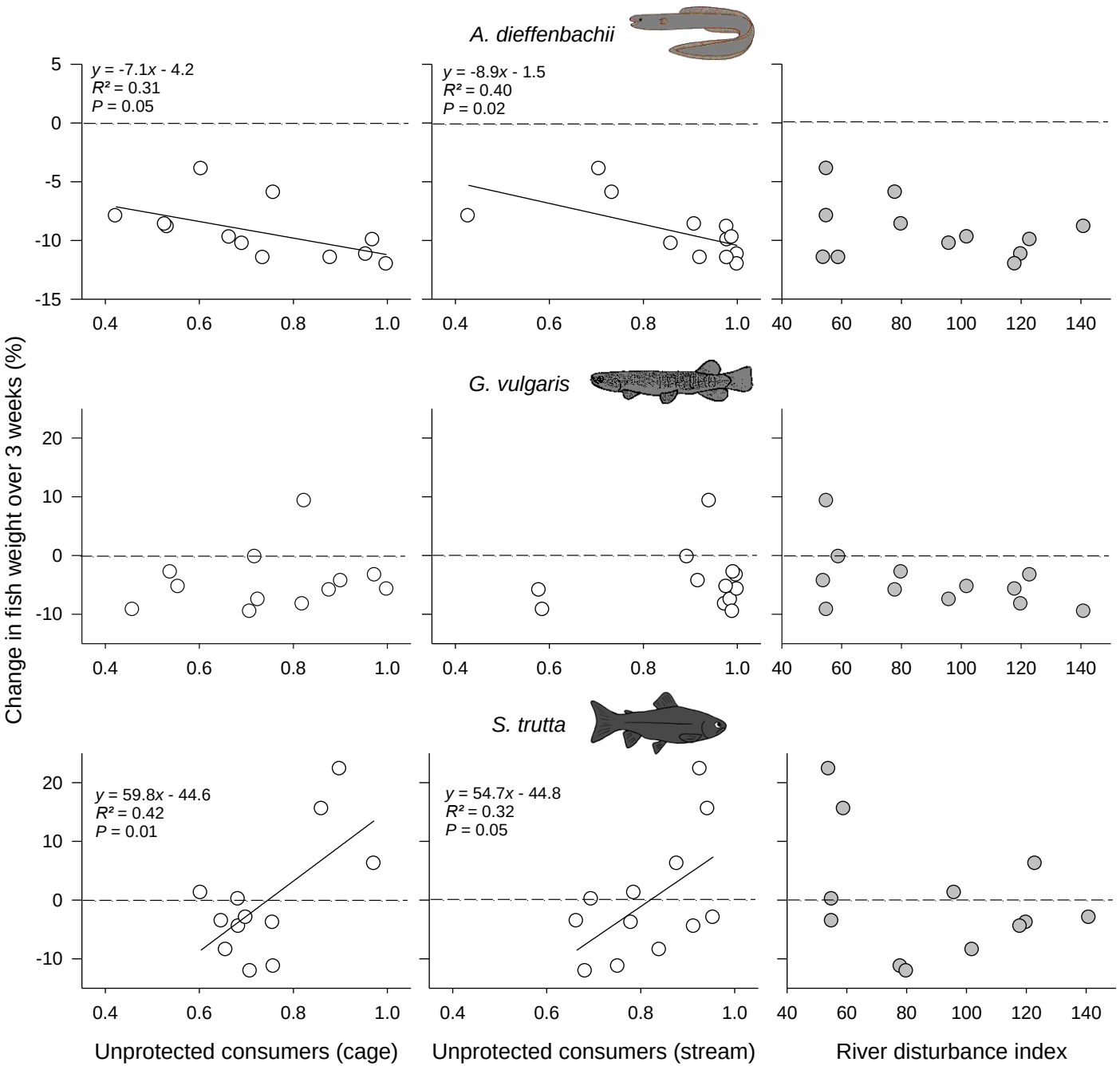


Figure 7. The change in weight of the three predatory fish species used in the cage experiment plotted against the proportion of unprotected consumers in the cages and streams. For comparison, changes in fish weight across the disturbance gradient are also shown. Only significant regressions are fitted.

Discussion

Environmental gradients clearly influence species distributions, abundance and interactions within food webs, although community ecologists have been criticised recently for ignoring this fact (McGill et al. 2006). Reducing the focus on pairwise species interactions and a return to assessing how traits govern niches across abiotic gradients has also been suggested (McGill et al. 2006). I have combined both approaches by first assessing variation in the niches of predatory fish species along a stream disturbance gradient and then linking variation in niches to differences in biotic interactions due to species traits (e.g., fish feeding behaviour, prey morphology) both within and between trophic levels. Moreover, I have examined whether prey community traits may exert bottom-up constraints on predator assemblages, and in particular, whether disturbance-induced prey assemblages could affect predatory fish composition.

Flood disturbance is a significant determinant of fish composition (Poff & Allan 1995). However, few researchers have attempted to link changes in fish community structure to variations in both flood disturbance and prey communities. Across the flood disturbance gradient, physical processes and prey assemblages should vary to produce conditions that may allow a species to dominate under certain conditions (i.e., species niche) but be outcompeted under other conditions. Fish species in this study exhibited distinct preferences across the disturbance gradient, with biomass of the five most common fish species peaking at different RDI values. Community regulation models (e.g., Peckarsky 1983, Menge & Sutherland 1987) predict that competition should be highest in stable habitats. Fish niche partitioning results are in general agreement with this prediction because niche overlap is extensive in stable habitats, so it is likely that multiple species are competing for a limited food resource. These models suggest that environmental harshness (i.e., disturbance) provides the primary gradient along which mechanisms regulating top trophic levels (i.e., predatory fish) vary. Therefore, I

assessed whether prey assemblage composition might provide a secondary gradient that could explain further variation in fish community structure.

The influence of disturbance on fish via prey assemblages

Flood disturbance events can influence species abundance at all trophic levels, and physical disturbance has been widely accepted as a strong structuring force in riverine food webs (Resh et al. 1988, Wootton et al. 1996, Lake 2000, Death 2008). Stream invertebrate communities in New Zealand are often driven by flooding (Winterbourn et al. 1981, Death & Winterbourn 1995), and as anticipated, I found prey community biomass decreased as habitats became increasingly disturbed. However, the severity of flood effects are often taxon-dependent, with molluscs and cased caddisflies (protected consumers) more susceptible to extirpation by disturbance than unprotected consumers such as mayflies and many dipteran species (Mackay 1992, Death 1996, 2008, Townsend et al. 1997a). I found strong taxon-dependent effects as protected consumer abundance declined at twice the rate of unprotected consumers as disturbance increased. Similarly, a simulated bed-moving flood led to 67% mortality of Conoesucidae caddisflies, the main family of New Zealand cased caddis (the impact of the flood-simulation on unprotected consumers could not be measured as too few were found) (Nyström & McIntosh 2003). Protected consumers are vulnerable to flood disturbance because of their heavy protective cases and limited mobility (Otto & Svensson 1980), but this is balanced by the resistance to predation offered by the cases (Otto & Johansson 1995, Wootton et al. 1996). The extent to which fishes preyed upon protected (and unprotected) prey appeared to be strongly linked to both fish species and their diet/mode of feeding.

New Zealand stream fishes feed on a common group of prey species but the relative proportion of each taxon in the diet typically varies such that trout species consume drifting

taxa, whereas benthic native fishes have more generalised diets (Cadwallader 1975, Sagar & Glova 1994, McIntosh 2000b). The benefit to prey of investing resources in morphological predator protection was assessed in the mesocosm predation experiment by measuring the foraging cost to fishes when consuming protected versus unprotected prey. Benthic-feeding fishes (i.e., eels and galaxiids) were equally proficient at consuming either prey type, eating a similar number of both in the experiment. In contrast, trout showed a strong preference for unprotected prey as they are predominately drift-feeding fishes (Fausch 1984) and unprotected prey are highly mobile and drift readily. Trout gained weight with increasing predation on this prey type in the mesocosm experiment and also gained weight in the *in situ* predation experiment when a greater proportion of the prey community was composed of unprotected consumers, regardless of the level of disturbance. These results suggest the indirect effect of disturbance on prey community structure, and not disturbance *per se*, were responsible for trout biomass peaking at intermediate levels of disturbance where unprotected prey had the highest relative abundance.

In highly disturbed waterways where the prey community was almost exclusively composed of unprotected prey, trout species were generally absent and *G. paucispondylus* was the dominant fish species. Trout generally have a negative impact on galaxiid abundance (e.g., Townsend & Crowl 1991, McDowall 2006), but it is likely that prey biomass is too low for them to exist in these habitats. *G. paucispondylus* was not tested in the predation experiments but in dietary studies, it is known to consume unprotected, soft-bodied prey in preference to protected taxa (Bonnett et al. 1989). There is almost no competition from trout for the unprotected prey resource in highly disturbed habitats, and consequently, *G. paucispondylus* can achieve high biomass and density (e.g., > 1.5 fish m^{-2}) at these sites. The increased drift propensity of unprotected prey at disturbed sites may be one mechanism that allows *G. paucispondylus* to achieve such densities where prey abundance is low, since non-

migratory galaxiids feed on both drift and benthos (Glova & Sagar 1989). Thus, a combination of disturbance-mediated prey assemblages and a reduction in competitive/predatory interactions with introduced trout probably results in the disturbed habitat niche observed for this species.

Predation on protected consumers should be reduced (in comparison to consumers that do not invest in morphological predator defences) for there to be a fitness advantage to organisms that exhibit this life-history strategy (e.g., Wootton et al. 1996), and since fishes lost weight in the mesocosm experiment when foraging on protected prey, my results support this suggestion. There was strong size selectivity by all fishes when foraging on protected prey but not when consuming unprotected taxa (see Fig. 5b). On average, a protected prey item contained half the AFDM of an unprotected individual (they also contain *c.* half the energy value, McCarter 1986), so size-selective behaviour is probably necessary to minimise foraging costs when feeding on protected prey. Nevertheless, a size-selective approach could still not offset the foraging costs for galaxiids and trout when consuming only protected prey because they both lost weight. As eels are energetically conservative fish (Helfman & Winkelman 1991) it was difficult to determine the cost of foraging on protected prey in the mesocosm experiment, as they may not feed for over a week when kept in captivity (D. J. Jellyman *pers. comm.*). Protected prey are a very important food source for stream-dwelling eels (Cadwallader 1975, Sagar et al. 2005), and made up over 98% of prey items consumed by longfin eels in some habitats (Jellyman 1996). The eel biomass quantile regression spline indicated that their ecological niche in stable streams coincided strongly with the highest biomass of protected consumers. Given there was also a strong niche overlap (i.e., likely competition) with brown trout for unprotected prey in these stable streams, protected taxa with limited mobility and a low propensity to drift, are likely to be a key food resource for benthic-feeding eels. Furthermore, protected prey are often most active at night (e.g.,

caddisflies, Elliott 1969) so may be more available to nocturnal feeding fishes such as galaxiids and eels than trout. The *in situ* predation experiment, which assessed changes in fish weight across a prey community composition/disturbance gradient supported this conclusion because eel weight significantly declined as the proportion of protected prey decreased. This relationship was not confounded by disturbance because there was no correlation between eel weight change and disturbance. Thus, eels responded not to disturbance directly, but to variation in their protected prey resource which was strongly influenced by disturbance.

In contrast to the other fish species, *G. vulgaris* did not exhibit strong dietary preferences in the experimental mesocosms where consumption rates were similar for both protected and unprotected prey. This finding is consistent with *G. vulgaris* having a general, opportunistic diet as postulated by Cadwallader (1975), and with the *in situ* experiment results where *G. vulgaris* weight showed no significant response to prey compositional variation. The association of *G. vulgaris* with more stable sites meant its niche overlapped greatly with that of trout, which is consistent with dietary studies showing these species are likely to be in direct competition for food and space (Cadwallader 1975, McIntosh et al. 1992). Whereas the biomass of larger fishes such as eels and trout is likely to be strongly influenced by disturbance-mediated prey assemblages, the biomass of smaller fishes (i.e., galaxiids) is likely to be affected by the abundance of both prey availability and the presence of larger fishes. The biomass of *G. vulgaris* is strongly affected by the presence and/or biomass of trout (Townsend & Crowl 1991, McIntosh 2000a), and high biomass (i.e., $\geq$ 1.5 g m^{-2}) only occurred in this study when trout were either absent or at low biomass (i.e., < 0.5 g m^{-2}). Thus, it appears that because of its generalised disturbance and feeding niches, *G. vulgaris* would once have dominated the intermediately disturbed streams in these systems. However, due to the introduction of trout, *G. vulgaris* is now widely displaced from these habitats by these large, drift-feeding fishes (McIntosh 2000a, Jellyman & McIntosh 2010).

The influence of prey traits on stream food-web interactions

Through predation, fishes can exert extreme selective pressures on lower trophic levels and shape the structure of prey communities (Paine 1966, Sih et al. 1985, Huryn 1998, Nyström et al. 2003). However, prey taxa can have morphological, behavioural and chemical defences that reduce their vulnerability to predation (McIntosh & Townsend 1994, Wellborn et al. 1996, Wootton et al. 1996). Consequently, the strength of predator-prey interactions can be influenced by prey vulnerability and whilst much research has been focussed on assessing how predators influence prey communities in stream habitats, less attention has been focussed on what prey attributes affect predator-prey interactions (see Power et al. 1992, Holomuzki & Biggs 2006 for notable exceptions).

The most common strategy of stream-dwelling primary consumers to reduce predation risk is to invest resources in a morphological defence (i.e., a protective case). Protected consumers in my study system did not grow large enough to escape predation by native or introduced fishes, but results from the *in situ* predation experiment showed the impact of predatory fishes on these prey types was significantly lower than on unprotected prey across the disturbance gradient. Their consistently lower predation risk was likely due to their protective cases, reduced abundance and small body size, since body size declines with increasing disturbance (Townsend et al. 1997a). In habitats with fish present, large-bodied species are more vulnerable to predation than smaller individuals (Pont et al. 1991, Wellborn 1994), so as habitats become increasingly disturbed, small protected consumers have a very low predation risk. It should be noted that as streams became more disturbed, there was increasingly more invertebrate biomass in the cages compared to the stream. Since the biomass of predatory fish was higher inside the cages than in the stream, the experimental cages may have been "attracting" invertebrates. It is important to acknowledge this

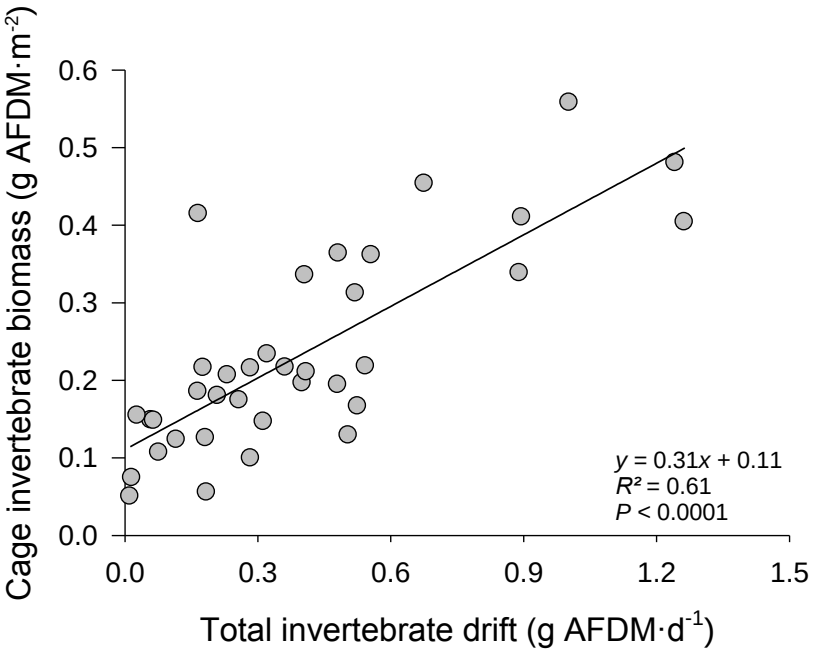
experimental artefact because if it was occurring, the results from the in situ cage experiment would be underestimating the impact of predatory fishes on prey communities.

As few studies have assessed how top-down and bottom-up processes vary across disturbance gradients, our understanding of their roles in structuring food webs are largely limited to more stable habitats (e.g., Wootton et al. 1996). In stable habitats, both top-down and bottom-up processes can be important in structuring food webs (e.g., Wootton et al. 1996, Nyström et al. 2003). Results of the *in situ* predation experiment support this contention since predatory fishes had an impact on both prey types, although the effect was reduced for consumers that invested resources in predator defence. My research also indicated that the impact of top-down processes became weaker as disturbance increased, regardless of consumer type. In summary, survey and experimental results showed that the bottom-up influence of disturbance on prey community structure determined not only predator composition but also the strength of top-down control because predator impact became weaker with increasing disturbance.

The processes that govern food-web structure in stable systems may be of less relevance in coming years as the frequency and intensity of climatic events causing disturbance are predicted to increase (IPCC 2001). In contrast, studies that assess how communities are assembled over large spatial scales and disturbance gradients are likely to become increasingly important for predicting ecosystem responses to global environmental changes. Many species that are adapted to stable habitats (e.g., protected consumers) have evolved traits that allow them to outcompete species that can exist in more temporally variable habitats (see Townsend & Hildrew 1994). Therefore, any increase in the disturbance regime is likely to result in a community shift that disproportionately impacts these consumers, and thus, the predatory fishes that utilise them as prey. From a food-web perspective, this study suggests that a catchment- or landscape-scale shift towards a more

disturbed state will probably result in reduced predator impacts and a weakening of top-down processes.

Appendices



Appendix 1. The relationship between total daily invertebrate drift and the biomass of invertebrates in *in situ* cages at the end of the experiment.

Plate 6. A very large longfin eel (*Anguilla dieffenbachii*) from a coastal Canterbury river.

Chapter Four

Interactive influences of habitat size and disturbance on top predator body size in stream fishes

Abstract

Body size is central to the trophic structure of food webs as it affects energetic demands, predator-prey feeding interactions and population density. Food webs are size-structured, so top predators play a key role in the structure and stability of communities. Studies of body size have largely focussed on individual food webs, with relatively little known about how body size changes over environmental gradients. Using surveys and field experiments, I investigated the effects of habitat size, disturbance and temperature on the body size of fish communities in New Zealand streams. A comparison of streams indicated that top predator body size decreased with increasing stream disturbance but increased in larger habitats and warmer streams. Model selection showed habitat size and disturbance were the most important drivers of top predator body size, and that there was a strong interaction between the two factors. Habitat size was the primary determinant of body size in stable streams but the effect of habitat size on body size weakened as habitats became more disturbed. An experimental reduction in habitat size decreased the proportion of large fish in stream reaches but did not alter total fish biomass. A large flood during the experiment briefly increased the proportion of top predators in disturbed streams. However, over an 11 month period, higher levels of flood-related disturbance led to reductions in their body size. This research indicates that larger top predators are likely to be most affected when habitats become smaller and disturbance increases. Because top predator effects on food webs are likely to vary with body size, relationships such as those found in this research should be incorporated into future

models of food-web responses to shifts in habitat size and disturbance regimes with changing climate conditions.

Introduction

Widespread and significant components of human-induced global environmental change have been impacts on the structure, composition and size of food webs (Lotze & Milewski 2004). Human-induced extinction and species exploitation are well documented, but our understanding of their impacts on food-web connections and community organisation is poor (Vitousek et al. 1997, Ives & Cardinale 2004). Within aquatic food webs, the impacts have been most severe at the highest trophic levels where the largest species, especially in fisheries, have been targeted (Pauly et al. 1998, Lotze & Worm 2009). The loss of these large top predators has restructured communities and altered food-web stability (Paine 1980, McCann et al. 2005, Gotelli & Ellison 2006). Yet a more complete and mechanistic understanding of top predator response to environmental change is still needed to better manage current and future human impacts on food webs, particularly in aquatic ecosystems.

Over 80 years ago Elton (1927) recognised that food webs were not randomly assembled because predators were larger than their prey. However, his early ideas linking body size and community structure languished until the 1980s when a resurgence in body-size related research was led by investigations of allometric body-size scaling relationships (e.g., Peters 1983, Roff 1986). We now know that body size is a fundamental driver of food-web structure and that it is strongly correlated with many food-web metrics (e.g., abundance, interaction strength) (Cohen et al. 2003, Woodward et al. 2005). Body size is also a particularly important determinant of food-chain length, because trophic position and the outcomes of predator-prey interactions are strongly size structured (Cohen et al. 1993, Brose et al. 2006). Although we know much from models and studies of single food webs (e.g.,

Cohen & Newman 1985, Woodward & Hildrew 2002), knowledge of the importance of top predator body size and what causes body size to vary across environmental gradients is still lacking. Researchers have suggested that ecology now needs research and experiments that disentangle competing or confounding environmental influences to better understand direct and indirect interactions on food webs (Agrawal et al. 2007). Therefore, my research focuses on disentangling the interactive effects of habitat size, disturbance and temperature on top predator body size in aquatic systems.

As humans continue to alter terrestrial and aquatic ecosystems through habitat destruction and fragmentation, and climate change (e.g., Rogers & McCarty 2000, Laurance et al. 2001), understanding how top predators are likely to respond to changes in habitat size is particularly important. In terrestrial and aquatic ecosystems, habitat size can be an important determinant of body size, especially for top predators (McNab 1963, Harestad & Bunnel 1979, Minns 1995). Top predators usually need to utilise larger areas than similarly sized herbivores to satisfy their energy requirements because less energy (per unit area) is potentially available from secondary producers than primary producers due to the energy losses at each trophic transfer (Harestad & Bunnel 1979, Pimm 1982). Whilst ecologists now realise that such strict hierarchical feeding chains are rare in nature (because omnivory is common among top predators, Vadeboncoeur et al. 2005), top predator habitat size requirements are still likely to be strongly related to resource quantity/prey availability. Thus, any reduction in habitat size may restrict predator growth rate, abundance and body size through a decrease in resource supply.

In addition to habitat size influencing top predator body size, the level of disturbance may also affect body size via direct and indirect pathways. Disturbance is "any relatively discrete event in time that removes organisms and opens up space which can be colonized by individuals of the same or different species" (Townsend 1989) and the frequency of extreme

climate events (e.g., floods and drought in streams) that cause high disturbance is predicted to increase under climate change scenarios (IPCC 2001). For example, disturbance reduces prey (i.e., benthic invertebrate) biomass and increases the patchiness of prey resources more in unstable than stable streams (Death 1996, Townsend et al. 1998). Heterogeneous prey distributions in disturbed environments can lead to reduced encounter rates between predators and prey (Weins 1976, Vogel & Beauchamp 1999), resulting in increased foraging costs (i.e., energy expenditure) for predators and reduced energy for growth (Stephens & Krebs 1987). Furthermore, prey availability is likely to be highly variable over time in disturbed environments, and for predators in disturbed habitats, I would expect that a continually disrupted forage base is likely to reduce predator abundance and body size. Thus, there is considerable potential for predator body size to be indirectly influenced by disturbance via its direct effect on prey availability.

At a global scale, climate warming is predicted to change runoff patterns and therefore base-flow discharge of streams and the frequency and magnitude of extreme events affecting them (IPCC 2001, Milly et al. 2005). In addition, as temperature directly affects the body size of animals (for a few notable exceptions see Atkinson 1995), an increase in temperature should decrease organism body size (in accordance with the temperature-size rule for ectothermic organisms, Atkinson 1994). A size decrease attributable to climate warming has already been observed in some fish and bird species (Daufresne & Boët 2007, Gardner et al. 2009). Surprisingly few studies have examined the impact of temperature variation on vertebrate body size (Daufresne et al. 2009), despite it scaling with many ecological properties (e.g., life history attributes, population carrying capacity, biotic interactions). Knowledge about how food webs and body size may respond to increases in temperature and reductions in habitat is lacking, and disentangling the effects of temperature from other potentially interacting factors is sorely needed.

I surveyed fish communities in streams to evaluate the effects of habitat size, disturbance and temperature on top predator body size. Streams form hierarchical networks that generally increase in size longitudinally (downstream), so large-scale drivers of top predator body size can be assessed across multiple environmental gradients within and across catchments. In conjunction with surveys, an *in situ* manipulation of habitat size was conducted to test four main top predator body size hypotheses. First, I predicted that top predator body size would be lower in smaller habitats because body size would be constrained by habitat size (H_1) due to the need for larger habitats to meet higher metabolic demands of larger organisms (McNab 1963). My second hypothesis was that body size would decline as stream disturbance increased (H_2) due to either the direct, or indirect, effects (e.g., a decrease in prey availability due to increased disturbance) of disturbance. Thirdly, in accordance with the temperature-size rule for ectotherms (Atkinson 1994), I predicted that body size would decrease with increasing water temperature (H_3). Finally, I hypothesised that all three main variables would interact to determine body size, such that habitat size would be most important in stable (benign) streams, but decrease in importance as a predictor of body size as streams become increasingly disturbed (H_4).

Methods

Study Area

Fish communities and physical attributes of streams were sampled at seventy four sites (Fig. 1) in Canterbury and Westland, contrasting regions of South Island, New Zealand from 2005 – 2009 (during spring, summer or autumn). Westland has high rainfall (often > 4600 $mm \cdot yr^{-1}$) due to prevailing westerly winds and high topographic relief (i.e., the Southern Alps rise from

sea level to 3000 m just 20 km inland), and has both high-gradient, flood-prone streams draining snowfields of the Alps, and low-gradient streams in podocarp-dominated, coastal rainforests. On the eastern slopes of the Southern Alps, rainfall and vegetation differ, dramatically. Rainfall in the Canterbury hill country rarely exceeds 1500 $mm \cdot yr^{-1}$ (decreasing with distance east) and vegetation is predominantly beech forest (*Nothofagus* spp.) and tussock grasslands.

Sites were selected based on the availability of background data, with the intent of producing a data set that had a large gradient of disturbance (achieved by having sites with contrasting flow regimes e.g., springs, braided rivers, etc.) and stream size for both regions. Fewer sites were sampled in Westland due to logistical constraints but a large disturbance and stream size gradient was still attained for the region. At each site, a single-thread 50 m survey reach was selected which was wadeable and less than 15 m wide (so it could be quantitatively electrofished). Within each reach, there needed to be a 25 m section containing at least one pool, run and riffle habitat for electrofishing. Sites were excluded if they: did not meet these criteria, were fishless, had pH values that may prohibit some fish species from being present (< 6 or > 8.5) or had high conductivity values (> 150 $\mu S \cdot cm^{-1}$; indicative of potential water pollution in these particular catchments).

Habitat surveys

Stream size was defined as stream cross-sectional area (m^2) and was calculated by averaging the two-dimensional area of five width-depth transects over a representative 50 m reach at each of the 74 study sites. Width transects were located at 10 m intervals and at least five depth measurements were made at equally spaced intervals across each transect. Catchment area was not used as a measure of stream size because the relationship between stream cross-sectional area and catchment area varied depending on whether streams were on the east or

west coasts, had surface-runoff, or were spring-fed (Appendix 1). Although water temperature was measured at each site at the time of sampling, measurements obtained may not be generally representative of site temperatures. Therefore, the temperature variable *SegSumT* [mean summer (January) air temperature] was extracted from the Freshwater Environments of New Zealand (FWENZ) river network model (Leathwick et al. 2008) and used. FWENZ is a comprehensive vector model of New Zealand rivers where each river is comprised of multiple segments (segments end at stream confluences). For each segment, various climate, geology, habitat and water chemistry variables have been modelled from remote-sensed national databases. The FWENZ *SegSumT* variable was validated against mean January 2008 water temperatures from 25 WT-HR loggers in the Rakaia and Waimakariri River catchments (Trutrak, Christchurch, N.Z). Given the large annual climate variation in this area, and that air temperature was being used to approximate site-specific water temperature, the model fit (R^2 = 0.51) was very good.

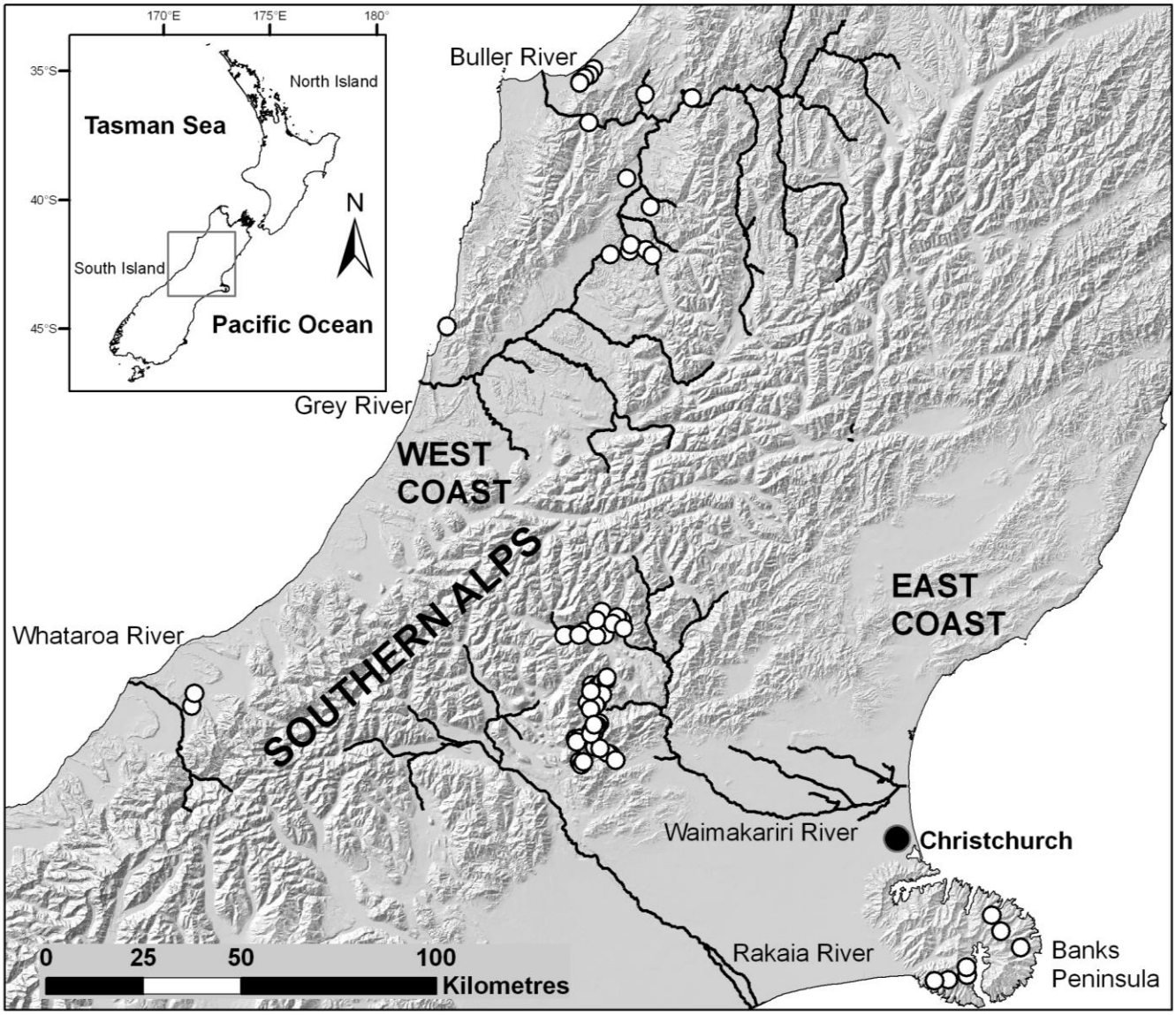


Figure 1. The location of survey sites (white circles) on the western and eastern sides of the Southern Alps, South Island, New Zealand. Only selected major rivers are identified.

Stream reach and channel stability, a measure that reflects stream disturbance regimes, was assessed using the river disturbance index (hereafter abbreviated to RDI) (Pfankuch 1975). This index estimates disturbance based on 15 categories that evaluate landscape, riparian and stream characteristics. The observer visually grades each category and the scores are summed to give an overall index score (RDI range: 38–152). Small numbers indicate a waterway is stable, whereas larger numbers signify that waterways are physically

unstable/highly disturbed. Greenwood & McIntosh (2008) found that the RDI was strongly correlated with substrate movement in stable and intermediately disturbed streams (RDI scores: 50-110), and my research (Chapter 2) indicates it correlates well with substrate movement across a much broader disturbance gradient (RDI scores: 57-141).

Fish communities

To investigate relationships between habitat-size, disturbance, temperature and fish communities (i.e., test $H_1 - H_4$ using survey data), at least 25 m of the 50 m survey reach (the length fished varied with stream width; longer distances were fished in narrow streams) was quantitatively three-pass electrofished with stop nets in place. All streams were surveyed using a Kainga EFM 300 backpack electrofishing machine (NIWA Instrument Systems, Christchurch, N.Z.) with 300 – 600 V pulsed DC (pulse width ~ 3 ms, 60 pulses s^{-1}), and with the operator moving in a downstream direction towards a 1 m wide push net (mesh size 3 × 2 mm ellipse). Electrofishing in a downstream direction is the most efficient method for capturing fish species in these streams (Jellyman & McIntosh 2010). All captured fishes were anaesthetized with 2-phenoxyethanol, measured [to the nearest 1 mm; fork length (FL) for salmonids and total length (TL) for other species], weighed and released. Fish densities were calculated using the maximum likelihood equations for three-pass depletion sampling (Cowx 1983).

A MANOVA was performed in R (R Development Core Team 2009) to determine the effect of habitat size (H_1), disturbance (H_2) and temperature (H_3) on the 74 fish communities surveyed. When the MANOVA was significant, univariate ANOVAs were conducted on the three response variables: density, biomass and maximum fish mass. Biomass and maximum fish mass were $\log_{10}$-transformed for all statistical analyses. The three response variables were further analysed using linear regression on the significant MANOVA factors. A fourth

response variable, maximum fish length was analysed with quantile regression (post-hoc), as the relationship with significant MANOVA factors appeared to be a limit response. Quantile regression calculates a linear function defining the upper or lower limits for a set proportion (i.e., 90^{th}, 95^{th} etc.) of a dependent variable's response to an independent variable (Cade & Noon 2003). It can therefore illustrate the upper limits of population and community responses to habitat gradients (Konrad et al. 2008). To be robust to major outliers, the 95^{th} quantile was fitted so the slope of the function was not disproportionately affected. The rigour of the plotted 95^{th} quantile slope was assessed using bootstrapped standard errors of its coefficient to test whether it differed significantly from zero.

The interaction between the three main factors (H_4) was assessed using an information-theoretic model-selection approach to select the two factors that had the greatest influence on maximum fish mass (Burnham & Anderson 2002). Maximum fish mass was then regressed separately against the two factors to identify models with the strongest support using the least-squares analogue of Akaike's Information Criterion, corrected for small sample size (AIC_c). The degree of support was considered for each model i using two values derived from AIC_c, Δ_i (i.e., $\Delta_i = AIC_{ci} - \min[AIC_c]$) and Akaike weights, w_i (i.e., $w_i = e^{(-0.5\Delta i)}/\Sigma e^{(-0.5\Delta i)}$). Furthermore, ij model pairs were compared using evidence ratio estimates (i.e., w_i / w_j) derived from Akaike weights.

Habitat-size experiment

To test directly whether body size in top predators decreased in smaller habitats (H_1), I manipulated the cross-sectional area of eight upper Waimakariri River catchment streams. Specifically, cross-sectional area was halved by installing a 25 m 'fence' orientated longitudinally down the centre of each stream. This fence restricted the lateral movement fishes could make, but fish were able to move unimpeded in and out of the fenced reach

during the experiment (see Plate 7). My initial experimental design included a habitat-size manipulation (fenced) reach and an unmanipulated control reach (Fig. 2), and was designed as a five-week experiment (mid-January to late February 2008). However, an 'out-of-season' rain/hailstorm caused a large, localised flood event that destroyed four habitat-size manipulation replicates (Fig. 2, Plate 7) at the end of week 2. However, the four remaining 'stable' streams still had intact habitat-size manipulations and could be used to evaluate habitat-size reductions on fish communities (with changes assessed against four unmanipulated control sections as originally envisioned – see Fig. 2). Fortuitously, the unmanipulated control sections of all eight streams were able to be compared to evaluate whether top predator body size declined in response to a major disturbance event (H_2).

In each of the eight experimental streams, a 75 m section was partitioned into three 25 m reaches: habitat-size manipulation, gap and control. The position (upstream/downstream) of the habitat-size manipulation and control reaches was randomly selected, and sections were always separated by the 25 m 'gap' reach. The longitudinal fence in the manipulated reaches was 25 m in length and was constructed from a layer of Nylex™ brown plastic trellis (95 cm high, 2 cm × 2 cm mesh) with an outer layer of Butlers™ woven green shadecloth (90 cm high, 2 mm × 2 mm mesh). The shadecloth was offset by 20 cm from the top of the trellis, resulting in a 15 cm skirt onto which gravel/cobbles could be placed to seal the base of the fence. The fence split the habitat-size manipulation reach into two equal sized reaches that restricted the habitat area available to fishes (see Plate 7). To hold the fences in position they were attached to three wires strung through six steel posts (1.65 m) spaced every five metres.

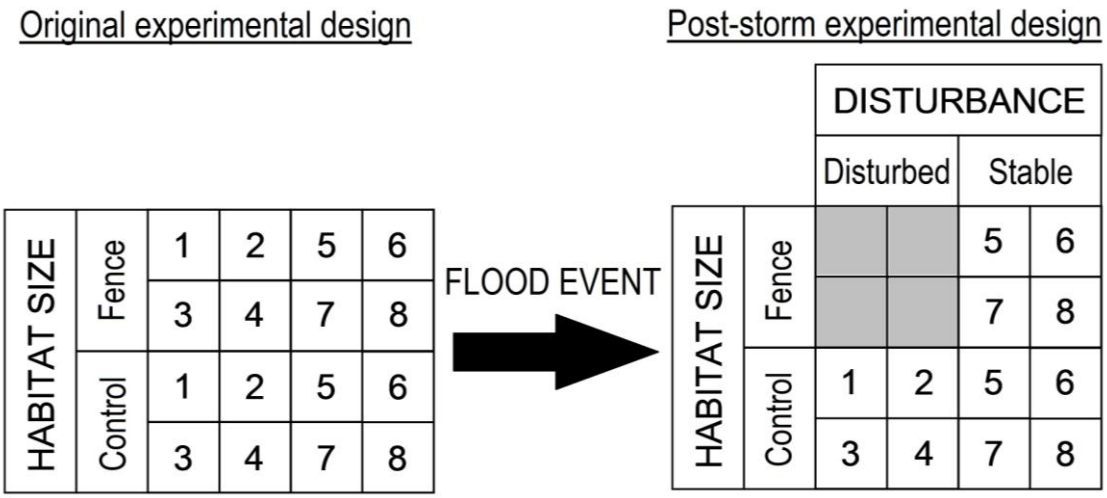
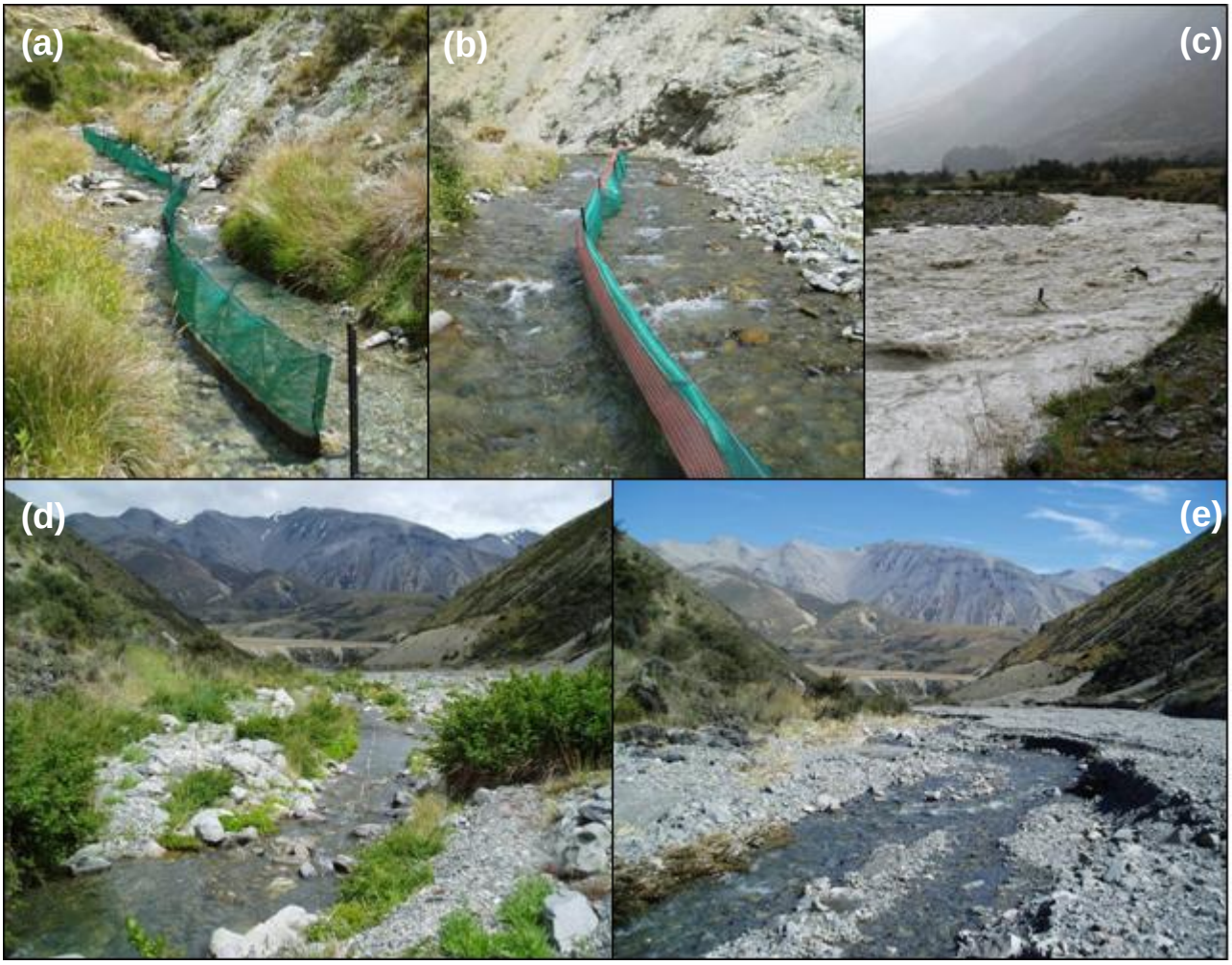


Figure 2. The original experimental design and that used following the large flood event that removed four (shaded grey) of the habitat-size replicates. In the habitat-size treatment, manipulated stream reaches are labelled as 'fence' because they were divided longitudinally by a 25 m *in situ* fence. Control reaches were unmanipulated. In the disturbance comparison, disturbed stream reaches were severely flood-impacted, whereas stable stream reaches did not flood. Numbers indicate the replicate streams that were assigned to each treatment combination.

The four habitat-size stream reaches varied in mean total width from 1.35 to 4.76 m; thus, each side of the manipulated reach ranged in width from 0.68 to 2.38 m. Reaches within each stream section did not change significantly in width, depth or temperature over the five week experimental period (one-way ANOVAs: Time effect, $P > 0.05$). Fish communities in control and manipulated reaches were initially sampled between 15 and 22 January 2008 using the electrofishing methods previously described. In habitat-size manipulation reaches, top and bottom electrofishing stop nets were put in place prior to the fence installation so fish did not escape sampling. Both halves of a divided stream were fished and the data pooled, so that fish communities in each manipulated reach could be compared to those in an unmanipulated reach. Large predatory galaxiids (*Galaxias vulgaris, G. paucispondylus* ≥ 110 mm) and trout (*Salmo trutta, Oncorhynchus mykiss* ≥ 150 mm) had a small piece of fin (anal fin – galaxiids, adipose fin – trout) clipped so they could be identified, subsequently. Sections were resampled after five weeks (23 February – 28 February 2008). Response variables were

the percentage change in fish biomass and the percentage change in the proportion of large predatory fishes over this period.

In the disturbance comparison, the four disturbed streams (mean width 3.2 m) did not differ significantly in size from the four stable streams (mean width 2.8 m) (one-way ANOVA, $P > 0.05$), and stream temperature (mean ± SE) did not differ significantly between disturbed (11.2 °C ± 0.7 °C) and stable (10.5 °C ± 0.6 °C) streams (one-way ANOVA, $P > 0.05$). The flood that occurred in all the disturbed streams was greater than three times the median flow, the benchmark used by Clausen & Biggs (1997) for assessing whether an ecologically meaningful flood had occurred. However, the storm event was so localised that it was not a major catchment flood, but was the largest recorded in the four disturbed streams during the five years of stream discharge monitoring (see Plate 7). Fish communities in the disturbed streams were sampled during the same period and using the same methods as the habitat-size stream reaches. Due to the flooding, fish movement was likely to have been much greater in these highly disturbed streams, so assessing changes in the proportion of top predators using the tagged fishes may well have strongly biased the results. Instead, the response variable 'change in top predator proportion' was assessed using electrofishing survey data, with the change in the proportion of top predatory fishes (still defined as galaxiids ≥ 110 mm, trout ≥ 150 mm) relative to small fishes (all fishes < 110 mm, trout < 150 mm) measured. Eels had not been fin-clipped in the habitat-size experiment, so were excluded from the disturbance comparison analysis.



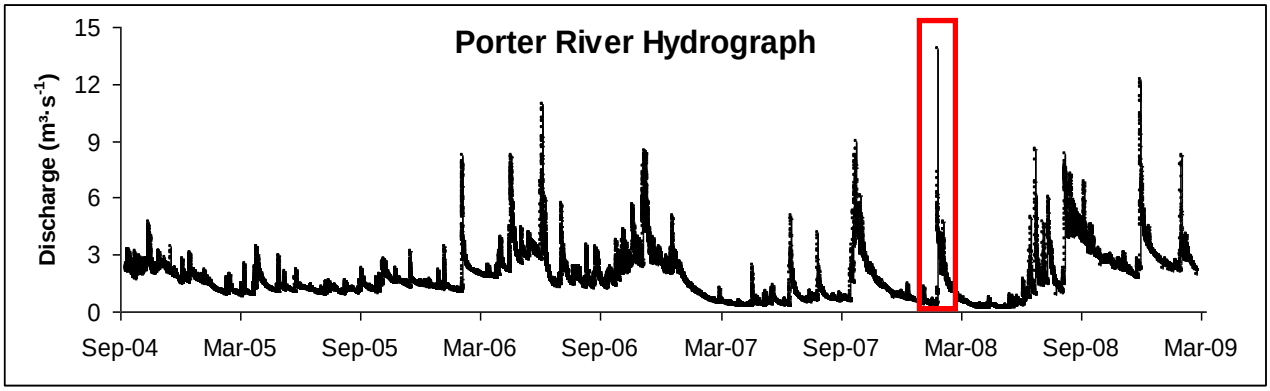


Plate 7. The habitat-size experiment and disturbance comparison. The habitat-size manipulation fence installed in Tim Stream (a). The fence installed in Porter River, before (b) and during (c) the flood event. Dry Stream, before (d) and after (e) the flood shown in photos taken from the same position in the control reach. The red rectangle on the Porter River hydrograph indicates the experimental period, and shows the large flood event that occurred.

As the interaction between habitat size and disturbance could no longer be evaluated with the modified experimental design (due to a lack of crossed habitat-size × disturbance replicates), the experiment was analysed using separate repeated measures multivariate analyses of variance (MANOVAs) on habitat-size and disturbance effects. In the MANOVAs, treatments were either manipulated or unmanipulated reaches for the habitat-size analysis, and stable or disturbed streams in the disturbance analysis. Treatment was nested within site for the habitat-size analysis because manipulated and unmanipulated reaches were in the same stream. The response variables for habitat size were the change in fish biomass or the change in the proportion of top predators over the experimental period. A change in the proportion of tagged fish was used for this analysis because electrofishing data showed the reach was not recolonised by other top predators (as previously defined) after the tagged fishes had departed. In the disturbance MANOVA, the same response variables (change in fish biomass and change in top predator proportion) were only tested against the treatment factor because time was not an explanatory factor of interest. MANOVA was used to control type I error rates when investigating two response variables with multiple ANOVAs.

Post-disturbance survey

In addition to the habitat size and disturbance comparison, an 11 month assessment of disturbance effects on fish communities and top predator body size (H_2) was conducted. With the exception of one stream that could no longer be accessed, the same control stream reaches used for the disturbance comparison were used. Streams were electrofished five times (*c*. 12 week intervals) during 2008 – 2009, to assess how fish communities and top predators responded/recovered to the February flood disturbance. The RDI was estimated on each sampling occasion, although one site could not be sampled during winter 2008 due to deterioration of the access track.

Changes in the proportion and body size of top predator fish were analysed using linear mixed-effects (LME) models with restricted maximum likelihood estimation (*nlme* package, R Development Core Team 2009). In the LME model for top predator proportion, species size thresholds were the same as for the habitat-size experiment. The top predator body size LME model used the largest fish (based on mass) captured during each of the electrofishing surveys as the response. The change in mass of the largest fish and the change in RDI (both relative to the previous sampling trip) were calculated for each 12-week period during the survey. LME models were initially used to investigate the effects of *a priori* disturbance categories [stable streams (i.e., 1 – 4) versus disturbed streams (i.e., 5 – 8) from Fig. 2] and time on the variables: change in $\log_{10}$-transformed maximum fish mass (Δ log maximum fish mass) and change in river disturbance index scores (Δ RDI). Based on model outputs, a third top predator body size LME model was fitted that replaced time as a factor with Δ RDI. The LME models allowed variation due to repeated stream sampling to be accounted for (random stream effect), whilst testing the main and interactive effects of the fixed variables. *F*-tests produced by *nlme* were used to determine significance levels.

Results

Fish communities

A total of 17 fish species were captured during the survey, almost all members of the regional species pool previously identified from the lotic areas surveyed (Appendix 2). Thus, a wide variety of fish communities were sampled in a broad range of fish habitats. Mean (± SE) species richness per site was 2.95 ± 0.17, with a maximum observed richness of eight species. A significant linear relationship was found between species richness and habitat size (R^2 =

0.31, $F_{1, 73}$ = 32.06, P < 0.0001, Appendix 3) but not between species richness and either disturbance or temperature. The level of disturbance ranged over the whole RDI scale (46 – 141), and habitat size varied from 0.08 – 4.52 m² (mean width: 0.81 – 13.9 m). Mean summer air temperature (*SegSumT*) ranged from 11.8 to 16.8 °C. The three factors, habitat size, disturbance and temperature, were not significantly correlated (all R < 0.09, P > 0.1).

MANOVA results indicated that disturbance, habitat size and temperature all had significant effects on fish communities (Table 1a), so univariate ANOVAs were used to assess the effects of all three explanatory variables on fish density, fish biomass and maximum fish mass (Table 1b). Fish density decreased significantly with increasing disturbance but did not change significantly across habitat-size or temperature gradients (Table 1b, Figs. 3a-c). A highly significant twentyfold decrease in fish biomass was found across the disturbance gradient, and smaller but significant increases in fish biomass at increasingly larger or warmer sites (Table 1b, Figs. 3d-f). Maximum fish mass differed significantly across gradients of all three explanatory variables, decreasing as streams became more disturbed, and increasing in larger or warmer streams (Table 1b, Figs. 3g-i). Ninety-fifth quantile regression indicated a negative limit response of maximum fish length with increasing disturbance (slope = -13.8 ± 1.0, t = -13.18, P < 0.0001; Fig. 3j). Positive limit responses of maximum fish length were observed across habitat-size (slope = 767.5 ± 139.9, t = 5.49, P < 0.0001; Fig. 3k) and temperature (slope = 247.2 ± 59.9, t = 4.13, P < 0.0001; Fig. 3l) gradients.

Table 1. Multivariate and univariate ANOVAs used to test the effects of disturbance (RDI), habitat size and temperature on fish communities. Univariate ANOVAs tested the effects of these three factors on the response variables: fish density, fish biomass and maximum fish mass; *df*, degrees of freedom; Pillai Trace, the multivariate test statistic; the coefficient of determination (R^2) values are given for the regression lines in Fig. 3 and the significance level (*P*) of the *F*-test statistic is displayed in bold if $P < 0.05$.

Source of variation	*df*	Pillai Trace	R^2	*F*	*P*
a) Multivariate test					
RDI	3, 64	0.63		36.60	**< 0.001**
Habitat size	3, 64	0.46		18.25	**< 0.001**
Temperature	3, 64	0.17		4.32	**0.007**
RDI × Habitat size	3, 64	0.12		2.92	**0.04**
RDI × Temperature	3, 64	0.05		1.16	0.33
Habitat size × Temperature	3, 64	0.03		0.57	0.63
RDI × Habitat size × Temperature	3, 64	0.02		0.34	0.79
b) Univariate tests					
Density					
RDI	1		0.09	7.03	**0.01**
Habitat size	1		< 0.01	0.02	0.89
Temperature	1		< 0.01	0.23	0.63
RDI × Habitat size	1			0.37	0.55
RDI × Temperature	1			0.18	0.67
Habitat size × Temperature	1			0.57	0.45
RDI × Habitat size × Temperature	1			0.32	0.57
Biomass					
RDI	1		0.56	109.38	**< 0.001**
Habitat size	1		0.06	10.92	**0.002**
Temperature	1		0.12	4.73	**0.03**
RDI × Habitat size	1			1.85	0.18
RDI × Temperature	1			0.81	0.37
Habitat size × Temperature	1			0.57	0.46
RDI × Habitat size × Temperature	1			0.34	0.56
Maximum fish mass					
RDI	1		0.26	50.68	**< 0.001**
Habitat size	1		0.28	54.44	**< 0.001**
Temperature	1		0.25	13.25	**0.001**
RDI × Habitat size	1			8.01	**0.004**
RDI × Temperature	1			3.52	0.06
Habitat size × Temperature	1			0.01	0.92
RDI × Habitat size × Temperature	1			0.00	0.95

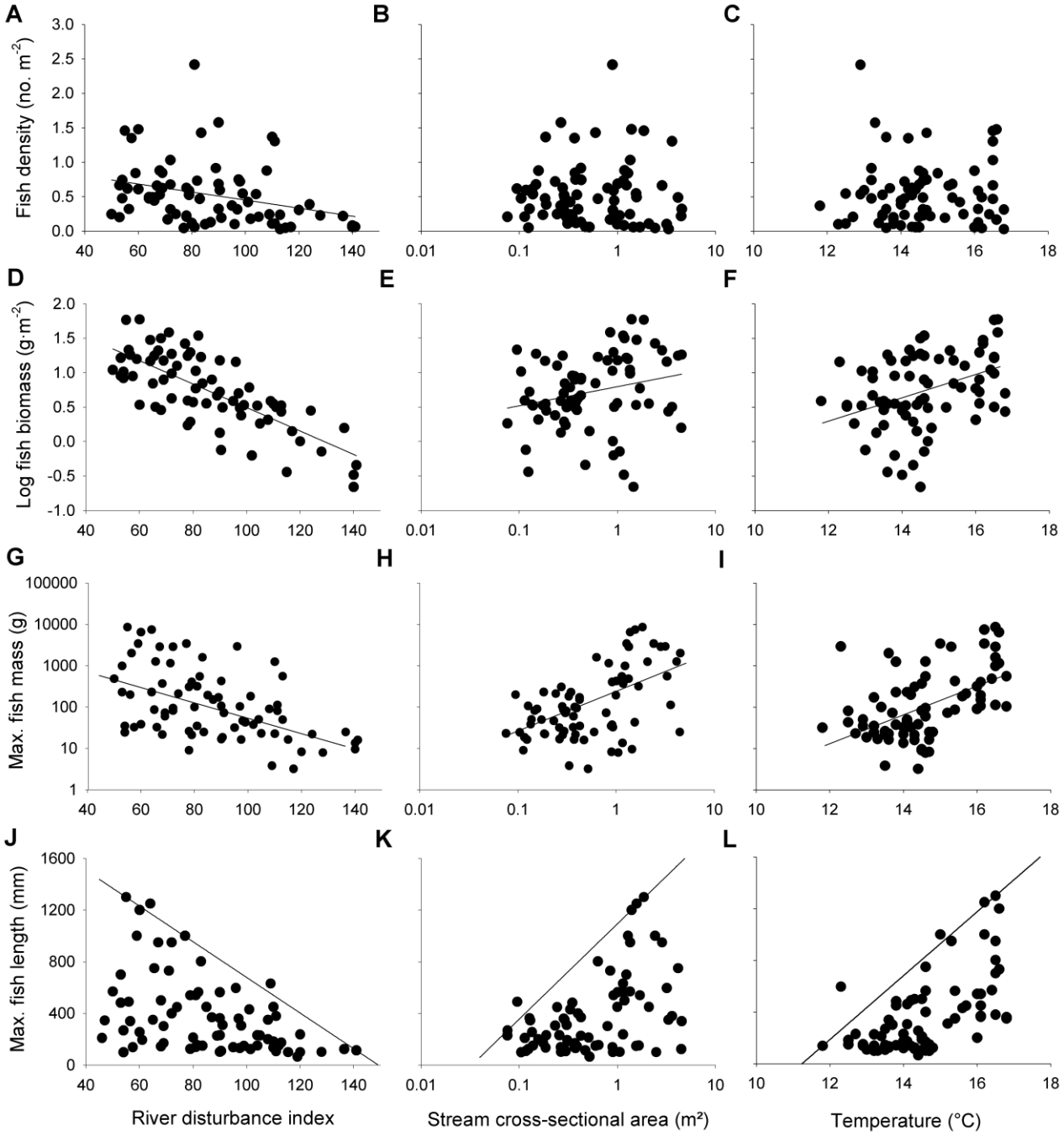


Figure 3. Relationships between disturbance (river disturbance index), habitat size (stream cross-sectional area) and temperature, and various fish community response variables. Only significant regression lines are shown; for maximum fish length, the line is the 95th quantile regression. R^2 and significance values are given in Table 1 or the text.

Table 2. Results of model-selection analyses for distinguishing between temperature (Temp), disturbance (RDI) and habitat size as the two main drivers of maximum fish mass. *K* is the number of estimated parameters (including the residual error term), *n* is the number of data points, R^2 is the coefficient of determination, AIC_c is Akaike's Information Criterion (with small sample size correction), and Δ_i is the AIC_c difference between a given model and that with the lowest AIC_c value. Evidence ratios (i.e., w_{top}/w_i) are relative to the top model in each set (i.e., that with $\Delta_i = 0.0$).

Model	*K*	*n*	R^2	AIC_c	Δ_i	w_i	Evidence Ratio
Maximum fish mass = Temp	3	74	0.25	- 42.8	38.1	0.00	184,494,177
Maximum fish mass = RDI	3	74	0.26	- 43.2	37.6	0.00	145,945,992
Maximum fish mass = Habitat size	3	74	0.28	- 45.2	35.6	0.00	54,414,740
Maximum fish mass = Temp + RDI	4	74	0.44	- 61.4	19.5	0.00	16,894
Maximum fish mass = Temp + Habitat size	4	74	0.40	- 56.6	24.2	0.00	180,116
Maximum fish mass = RDI + Habitat size	4	74	0.54	- 75.8	5.1	0.07	13
Maximum fish mass = Temp × RDI	5	74	0.49	- 66.5	14.3	0.00	1294
Maximum fish mass = Temp × Habitat size	5	74	0.40	- 54.4	26.4	0.00	541,795
Maximum fish mass = RDI × Habitat size	5	74	0.58	- 80.8	0.0	0.93	1

Model selection indicated that habitat size followed by disturbance were the most important drivers of maximum fish mass. The best model included an interaction between habitat size and disturbance, and this factor combination garnered 93% of the total model weight (Table 2). Without the interaction term, the model explained only a small proportion (0.07) of the candidate-set Akaike weight total. Furthermore, the model with an interaction term was 13 times more likely than a model without one (i.e., based on model evidence ratios). The relationship between maximum fish mass and the habitat size × disturbance interaction was then plotted using a three-dimensional scatter plot fitted with a Lorentzian function ($R^2 = 0.56$, $F_{4, 73} = 22.01$, $P < 0.0001$), to illustrate how the interaction varied along disturbance and habitat-size axes (Fig. 4). The interaction between disturbance and habitat size indicated that fish reached their maximum mass when habitats were large and stable (Fig. 4). The effect of habitat size was minimal in highly disturbed streams, and conversely, the effect of disturbance was minimal in small streams (Fig. 4).

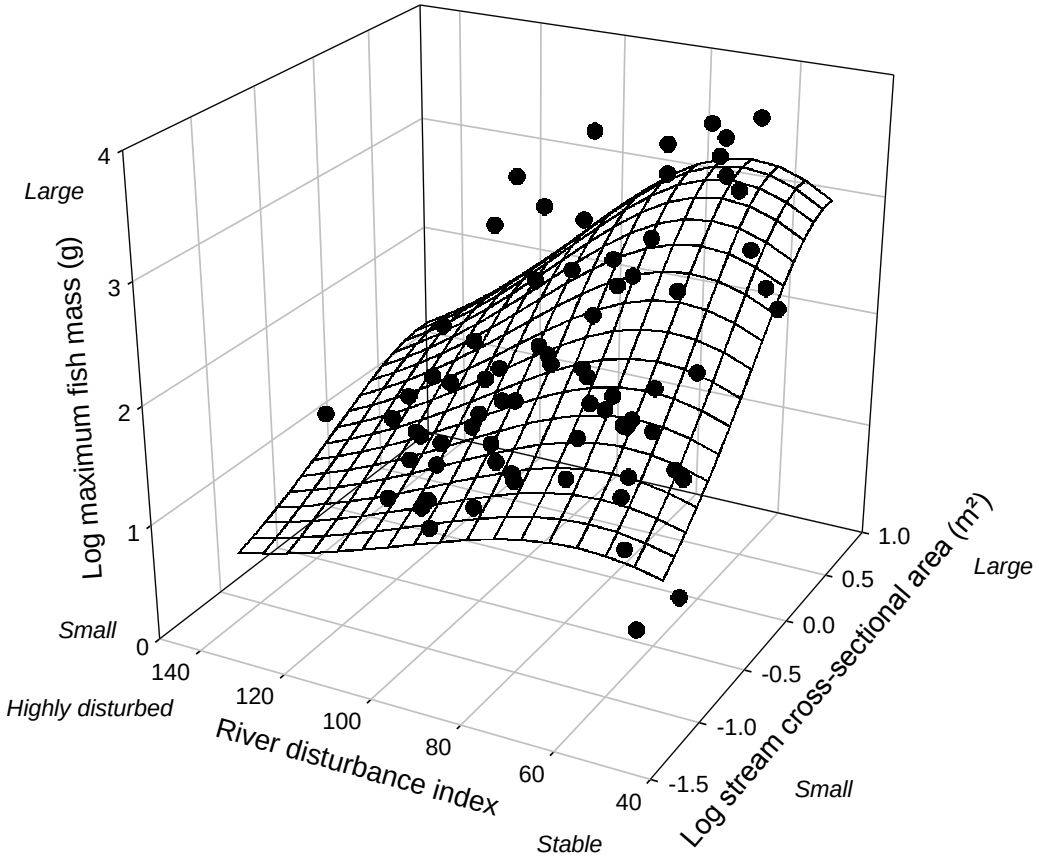


Figure 4. Three-dimensional scatter plot fitted with a Lorentzian function ($R^2 = 0.58$, $F_{4, 73} = 22.01$, $P < 0.0001$) to illustrate how the response of maximum fish mass (log maximum fish mass) changes across disturbance (RDI) and habitat-size (log stream cross-sectional area) axes.

Habitat-size experiment

Habitat size and disturbance had contrasting effects on fish community structure (Table 3, Fig. 5). In habitat-size analyses, results from univariate ANOVAs (on significant MANOVA factors) indicated that fish biomass did not change significantly over the five weeks in manipulated (fence) reaches compared to unmanipulated (no fence) reaches (Table 3b, Fig. 5). The proportion of top predators (as indicated by the change in the number of large, tagged fish relative to smaller, untagged fish) in the manipulated reaches changed significantly over the experimental period compared to unmanipulated reaches (Table 3b). Top predator proportion decreased by 74% in the manipulated reaches over the five weeks compared with only a 13% decrease in unmanipulated reaches (Fig. 5).

The disturbance comparison showed that average fish biomass differed significantly between stable and disturbed streams (Table 3d). Biomass decreased by 48% in disturbed streams compared to a 2% increase in stable streams (Fig. 5). During the experiment, the proportion of top predators (as indicated by the change in the number of large fish relative to small fish from electrofishing data) increased by 11% in disturbed streams (Fig. 5), an increase that was significantly greater than that found in stable streams (Table 3d).

Table 3. Results of repeated measures multivariate and univariate ANOVAs testing the response of fish communities in the habitat-size experiment. Habitat-size analyses were tested with the treatment effect nested within site (see methods). *df* is the degrees of freedom, Pillai Trace is the multivariate test statistic and the significance level (*P*) of the *F*-test statistic is displayed in bold if $P < 0.05$.

Source of variation	*df*	Pillai Trace	*F*	*P*
HABITAT SIZE				
a) Multivariate test				
Time	2, 11	0.16	1.07	0.38
Treatment (Site)	2, 11	0.45	4.58	**0.04**
Time × Treatment (Site)	2, 11	0.51	5.82	**0.02**
b) Univariate tests				
Biomass				
Time	1		0.01	0.91
Treatment (Site)	1		0.93	0.35
Time × Treatment (Site)	1		0.42	0.53
Top Predator proportion				
Time	1		1.47	0.25
Treatment (Site)	1		8.34	**0.01**
Time × Treatment (Site)	1		4.77	**0.049**
DISTURBANCE				
c) Multivariate test				
Treatment	2, 5	0.89	19.77	**0.004**
d) Univariate tests				
Biomass				
Treatment	1		6.27	**0.046**
Top Predator proportion				
Treatment	1		40.28	**< 0.001**

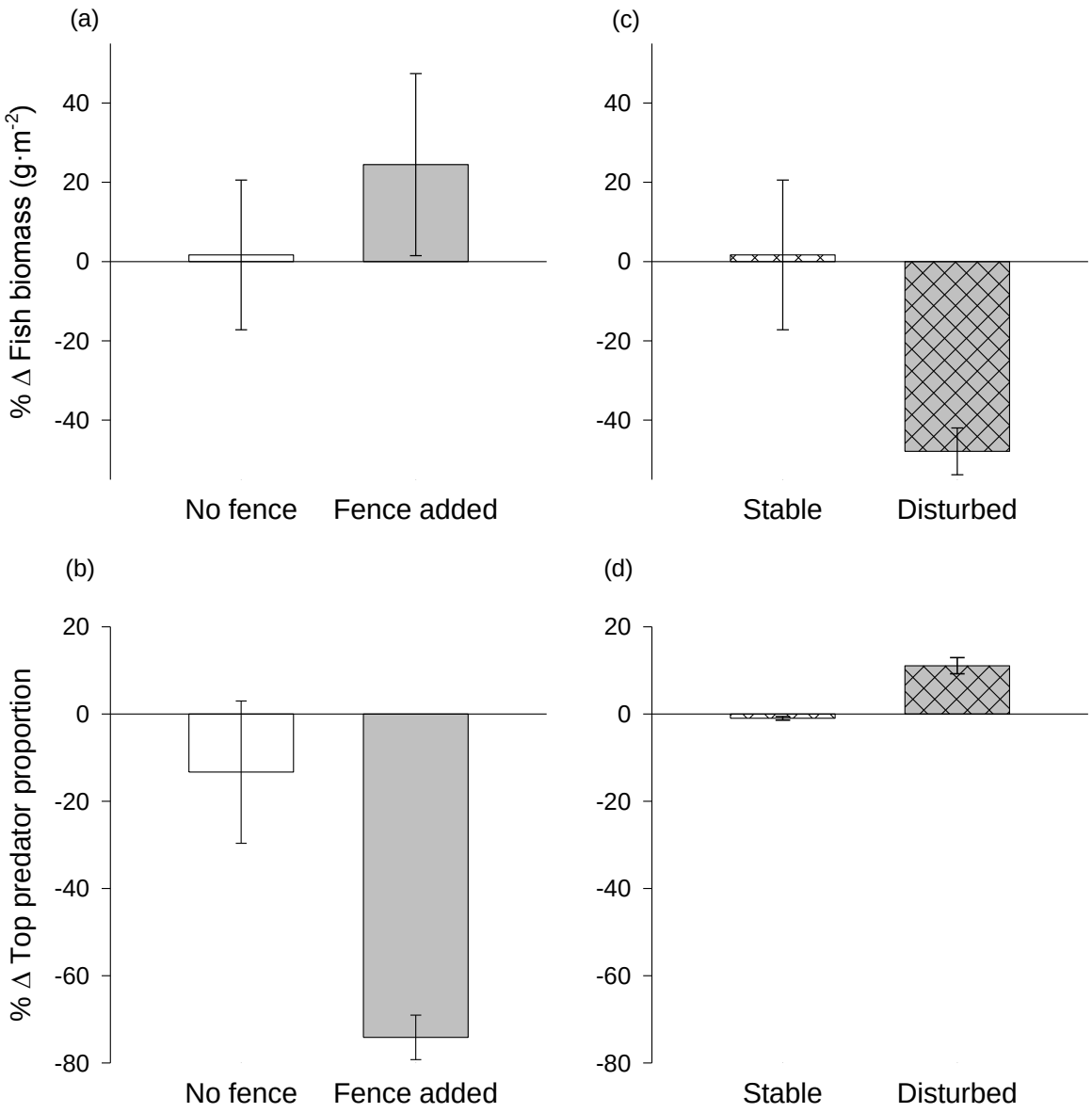


Figure 5. The percentage change (% Δ) in fish biomass and the proportion of top predators in the habitat-size experiment and the disturbance comparison. The change in each index is for the five week experimental period. The response variable, % Δ Top predator proportion, was calculated differently for graphs (b) and (d) (see methods). For clarity, habitat-size graphs are not hatched and disturbance graphs are hatched.

Post-disturbance survey

In contrast to the results of the habitat-size experiment, no significant change was found in the proportion of top predators (galaxiids ≥ 110 mm and trout ≥ 150 mm) in fish communities over the 11-month survey period (LME model: Top predator proportion × Time effect, $P > 0.05$).

In top predator body size analyses, LME models indicated that neither disturbance category (stable versus disturbed streams from the disturbed stream comparison) nor time significantly affected the Δ RDI. Δ RDI was therefore treated as a factor and not a response (Table 4a). Similarly, neither disturbance category nor time significantly affected the response variable Δ Maximum fish mass (Table 4b). However, a significant linear relationship was found between Δ RDI and Δ Maximum fish mass, indicating that maximum fish mass decreased with disturbance (Figure 6, Table 4c, see also Appendix 4 for a comparison of top predator body size and disturbance over time). The interaction between disturbance category and Δ RDI also had a significant effect on maximum fish mass (Table 4c). Linear regression analysis for each disturbance category showed there was a significant relationship between Δ Maximum fish mass and Δ RDI for stable sites (black circles, Fig. 6) ($R^2 = 0.71$, $F_{1, 15} = 34.76$, $P < 0.0001$), but not for disturbed sites ($R^2 = 0.10$, $F_{1, 10} = 1.02$, $P = 0.34$).

Table 4. Linear mixed-effects (LME) models tested the effects of explanatory factors on the selected response variable (either Δ RDI or Δ Maximum fish mass) whilst accounting for variation due to repeated stream sampling. Model simplification was used to estimate the *F* statistic and its significance level (*P* value) for the fixed effects and their interaction. *df* = degrees of freedom, *P* values < 0.05 are indicated in bold.

Source of variation	Numerator *df*	Denominator *df*	*F*	*P*
a) Δ RDI				
Disturbance category	1	5	0.90	0.39
Time	3	14	1.06	0.40
Disturbance category × Time	3	14	1.97	0.17
b) Δ Maximum fish mass				
Disturbance category	1	5	1.57	0.27
Time	3	14	1.99	0.16
Disturbance category × Time	3	14	2.61	0.09
c) Δ Maximum fish mass				
Δ RDI	1	18	31.89	0.001
Disturbance category	1	5	0.54	0.49
Δ RDI × Disturbance category	1	18	9.25	0.007

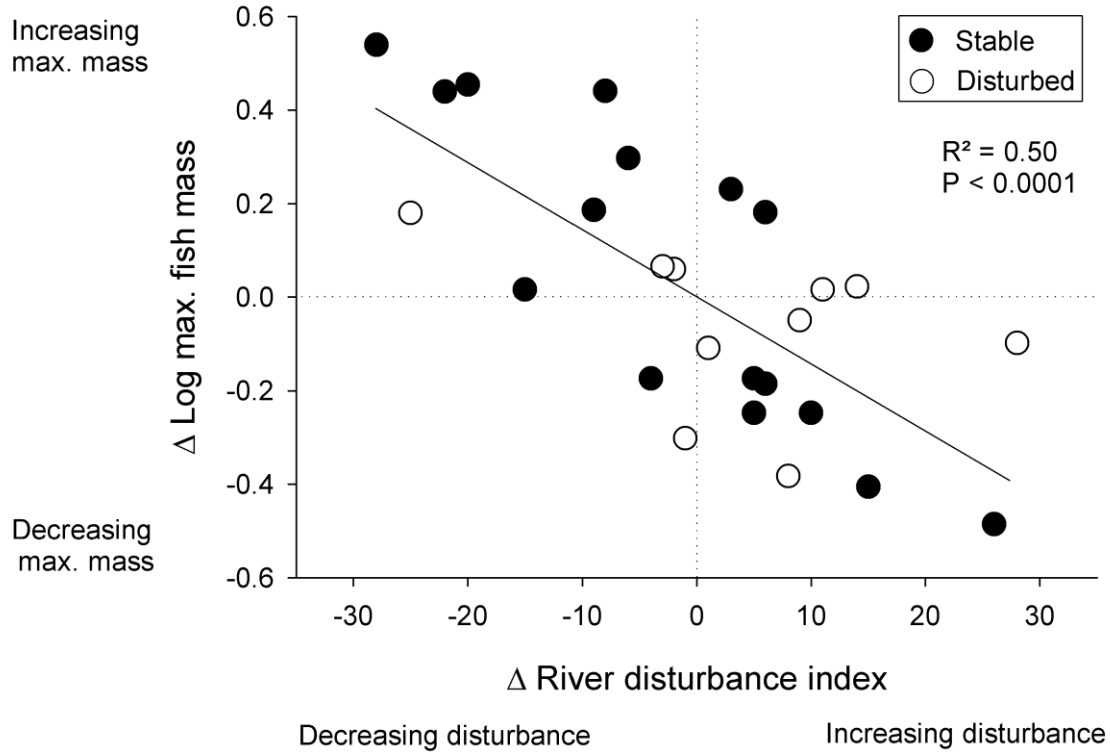


Figure 6. Relationship between the change in maximum fish mass and the change in river disturbance index (Δ RDI) for the 11 month disturbance impact survey. The regression line fitted is for all data points. Statistics for stable and disturbed regression lines are reported in text.

Discussion

Top predator abundance and body size are two key determinants of food web structure in aquatic and terrestrial ecosystems (McCann et al. 2005, Woodward et al. 2005), yet little is known about what influences these fundamental community attributes. My results show that top predator body size can vary with habitat size, disturbance and temperature, but not necessarily in an additive, linear manner. Habitat size is likely to act as the primary determinant of top predator size in these systems because larger predators (such as fish in this study) require bigger habitats to satisfy their energy requirements (e.g., Harestad & Bunnel 1979). The body size of top predators increased as habitats became larger, particularly in the absence of disturbance. Disturbance provided a secondary constraint on top predator body size, possibly due to reductions in prey abundance in increasingly disturbed streams (Death & Winterbourn 1995, Death & Zimmermann 2005, Chapter 3). No fish greater than 25 g were found at highly disturbed sites (RDI scores > 115). Moreover, in a subset of the 74 sites, McHugh et al. (2010) found that food chains became shorter in disturbed streams because of prey limitations for top predatory fishes, especially in cases with reduced availability of intermediate predators (i.e., predatory invertebrates). In contrast to habitat size and disturbance, temperature affected top predators in a linear, less-interactive manner.

The influence of temperature on predatory fish body size

Because thermal tolerance of animals generally has a negative relationship with body size, a major effect of climate warming is predicted to be greater extinction frequencies at higher trophic levels and a resultant shift in the size-structure of consumers towards smaller species (Petchey et al. 1999, Strecker et al. 2004, Holzapfel & Vinebrooke 2005, Xenopoulos & Lodge 2006). Over the last 25 years, the proportion of small fishes (< 100 mm) in large French rivers has increased at the expense of larger fishes (Daufresne & Boët 2007),

suggesting that higher trophic levels are more sensitive (than lower levels) to climate warming (e.g., Strecker et al. 2004, Daufresne et al. 2009). Thus, I anticipated that the body size of top predatory fishes would decrease with increasing temperature. However, in contrast to my temperature-body size hypothesis, I found that maximum body size increased as temperature increased. The temperature-size rule (on which my hypothesis was based) predicts that organisms should grow large in colder environments because growth efficiency decreases with increasing environmental temperature (Atkinson 1994). A literature review of this rule found little evidence to support this growth efficiency assumption (as the majority of studies found that growth efficiency was either positively related or insensitive to environmental temperature) and questioned the generality of this rule (Angilletta & Dunham 2003). The temperature-size rule is largely based on individual species responses to temperature changes, but a negative temperature-body size relationship in freshwater fishes has been used to further the generality of the temperature-size rule to the community level (e.g., Daufresne et al. 2009). My results question this community-level generalisation for freshwater fish communities, and furthermore, I expect that fish communities in many other systems would not support this contention. For example, within a catchment, streams become warmer and larger as they flow towards the sea (due to a decrease in latitude and their dendritic network configuration) and since the biggest fishes are found in large habitats, it is quite probable that a trend whereby the largest predators are present in warm, coastal waterways will be common globally.

Whilst such a trend may contrast some studies and/or theory about body size and temperature, this research does not conflict with predictions relating to changes in top predator body size with global temperature increases (e.g., Daufresne & Boët 2007, Gardner et al. 2009). Current body size-temperature relationships can only be sustained if the productivity of a system can increase with temperature, and if it cannot, then top predatory

fishes will eventually reach a "tipping-point" when productivity cannot meet their metabolic requirements (or when temperature exceeds tolerable thresholds for particular life stages, e.g., egg development). These tipping-points are likely to be system-specific, varying with predatory fish species, prey community traits and environmental variables. Thus, making general predictions about how long "climate-warmed" food webs may be able to sustain large predators is likely to be particularly difficult.

The dual influences of habitat size and disturbance on predatory fish body size

The positive relationship I found between top predator body size and habitat size was expected given that larger organisms require bigger habitats to meet their metabolic demands (i.e., allometric scaling relationships; Peters 1983, Minns 1995). Such a relationship predicted by ecosystem-size theory suggests that longer food-chains, and therefore larger top predators, will occur as habitat size increases (Post et al. 2000, Post 2002). In lake and terrestrial ecosystems, food chains lengthen through the addition of new top predator species (Schoener 1989, Post et al. 2000), and my finding of a positive species richness-habitat size relationship supports this mechanism (see also McHugh et al. 2010). However, stream food webs often have a limited pool of fish species to draw upon, especially on islands such as New Zealand where the fish fauna is not diverse, so some top predator species may be ubiquitous across entire habitat-size gradients. Species data indicated that as stream size became larger, species richness increased through the addition of smaller fish species (e.g., *Gobiomorphus* spp., bullies) and not through the addition of new top predators. The largest top predator species (*Anguilla dieffenbachii*, the longfin eel) was present in the smallest and largest stream surveyed (see Appendix 2), and was able to increase its body size as stream size increased. Its ability to increase its body size in larger habitats, often results in longfin eels having the highest trophic position of any predatory fish species when present (see McHugh et al. 2010).

A potential mechanism for one species maintaining the highest trophic position across the habitat size gradient may be that top predatory stream fishes are better adapted to increasing their body size in response to changes in habitat size (compared with vertebrate predators in other ecosystems). The flexible, indeterminate growth patterns characteristic of many fish species (Sebens 1987) may allow them to better exploit habitats with high spatiotemporal variability, such as streams. Furthermore, top predatory fishes in most New Zealand streams are generalist, opportunistic predators (McIntosh 2000a), so with less defined dietary preferences than top predators in many other ecosystems, they may be able to exploit a much wider range of food resources (Arim et al. 2007, 2010).

Conversely, reductions in habitat size, whether through natural or anthropogenic processes (e.g., droughts, water abstraction etc.), can also reduce the sizes of top predators in a system (Walters & Post 2008). As top predators are characterised by traits such as large body size, low density and slow reproduction rates they will take disproportionately longer to recover from habitat compression than smaller species (Raffaelli 2007, Worsfold et al. 2009). This has important implications for food-web structure as food-web stability and predation pressure on lower trophic levels are predicted to decrease when top predator size is reduced (McCann et al. 2005, Andersen & Pedersen 2010). Moreover, I found that habitat size constrained maximum fish length, indicating that large predators could not persist in small habitats, and was likely due to either the metabolic demands of larger fishes not being satisfied and/or increased predation risk from terrestrial predators (e.g., birds) in these small habitats (Allouche & Gaudin 2001, Steinmetz et al. 2003).

The effect of experimentally reducing habitat size for top predators was investigated by splitting streams longitudinally with an *in-situ* fence. This manipulation had a significant effect on the presence of large predatory fishes, with a 74% reduction in their proportion. As the removal of top predators did not significantly change the biomass of fish communities,

small fishes must have colonised the newly vacated habitats. Fish biomass was not expected to change significantly because this experiment reduced neither total habitat size nor prey density, merely the way the habitat area was configured. These experimental results concur with the field survey patterns and showed that a decrease in habitat size severely reduced a system's ability to sustain large predatory fishes. Furthermore, these results demonstrate that as habitats shrink, the largest predators are lost first, a trend which has been observed for some time in terrestrial systems (Diamond 2001).

My analyses showed that habitat size was an important factor influencing top predator body size in study streams, but disturbance also played a major and interacting role. As hypothesised, I found maximum predator size (and also fish community density and biomass) decreased with increasing disturbance. The biomass of predatory fishes that these systems support has been strongly linked to prey availability (Huryn 1998), so decreases in fish biomass, density and body size may be due to reduced resource availability in more disturbed habitats. Small fish body size in highly disturbed habitats may also be due to the life-history traits of members of the prey communities present (Townsend et al. 1997). Prey species in these streams are generally small because organisms that mature quickly and/or have many offspring per reproductive cycle and/or have many reproductive cycles per year are resilient to floods and droughts (Townsend & Hildrew 1994). Consequently, prey abundance is likely to be low and spatiotemporally variable in these flood-prone habitats. It is likely that galaxiids are able to persist under low prey biomass conditions because their benthic-feeding behaviour reduces energy expenditure during feeding, whilst drift-feeding species, such as trout, require a larger prey resource to offset the cost of their energetically-expensive feeding method (Fausch 1984). Thus, the small and variable prey resource in these highly disturbed streams is almost certainly inadequate for predators to grow large, if they have the intrinsic ability to do so.

The effects of disturbance on fishes are difficult to separate from those due to variation in resource availability when these streams become highly disturbed (Death & Winterbourn 1995, McHugh et al. 2010) because factors such as substrate movement, turbidity and high water velocities affect fish predation and resource availability. The limit response from quantile regression analysis found that maximum fish length was linked to disturbance, and indicated that fish could only grow to a certain size because of the constraints imposed by the level of disturbance. Whilst the large-scale survey of fish communities was unable to determine whether disturbance or resource availability was the major driver of top predator body size, the limit response between disturbance and body size showed that disturbance was capable of limiting body size across the entire habitat size gradient. Previous studies testing food-chain length hypotheses have found that disturbance plays a more important role than resource availability (e.g., Pimm 1982, Pimm & Kitching 1987, Spencer & Warren 1996, Post et al. 2000, McHugh et al. 2010), and similarly, my results suggest that disturbance may be more important than resource availability in determining top predator body size. The intensity and frequency of disturbance is likely to be strongly related to predation risk for large fishes because unstable habitats offer little in-stream cover/protection from terrestrial threats (e.g., avian predation). Therefore, the presence of suitable cover (largely controlled by disturbance/stability) may be a primary determinant of top predator occurrence, and resource availability only a secondary factor influencing habitat suitability.

The effect of disturbance on top predators was further assessed in a comparison of stable and disturbed streams used in the modified habitat-size experiment. In agreement with survey patterns, results from the disturbance analysis showed that fish biomass decreased by over 40% in disturbed streams compared to streams not flooded during a major storm. However, the proportion of top predators increased in disturbed streams due to the

disproportional loss of small fishes (relative to top predators), a finding contrary to the field survey patterns which showed top predator body size decreased with increasing disturbance. Whilst this experimental result appears to suggest that under certain conditions (e.g., over short time periods) high levels of disturbance can have a positive effect on top predators, this is unlikely, as a reduction in prey (both invertebrates and small fishes) should still negatively effect top predators although it may take longer for this effect to be detected compared to smaller fishes. Moreover, the post-disturbance survey did not detect a positive effect of disturbance on the proportion of top predators in these same streams over 11 months. Similar to the field survey results, the temporal site comparison from the post-disturbance survey showed that top predator body size increased as disturbance weakened, and vice versa. Therefore, a positive disturbance effect for top predators is unlikely (even over short periods), as prey supply and potentially competition from smaller fishes, is expected to have the greatest influence on the body size of top predators (Elliott 1994).

Habitat size and disturbance influence top predator body size through different mechanisms, so their interaction was of particular interest in this research. Habitat size had a minimal effect on top predators in highly disturbed streams, and the effect of disturbance on body size was negligible in small streams. Therefore, the largest top predators were in large, stable streams. As habitat size increases, ecosystem-size theory predicts that longer food-chains with larger top predators should occur, independent of any resource availability effect (Post 2002). This interaction of habitat size and disturbance in determining top predator body size concurs with the predictions of ecosystem-size theory for two reasons. First, the largest top predators were present in the largest streams across the disturbance gradient (although the effect was most evident in the stable streams). Second, resource availability (i.e., prey) declines across the disturbance gradient in these streams (Death & Winterbourn 1995, McHugh et al. 2010, Chapter 3), yet body size was invariant along the disturbance gradient

indicating resource availability had no effect on body size in these small streams. Ecosystem-size effects should be weakest in small streams (due to lower species richness of fishes in smaller habitats, see Appendix 3) so if an effect of resource availability on top predator body size was occurring, it should have been most apparent at these sites.

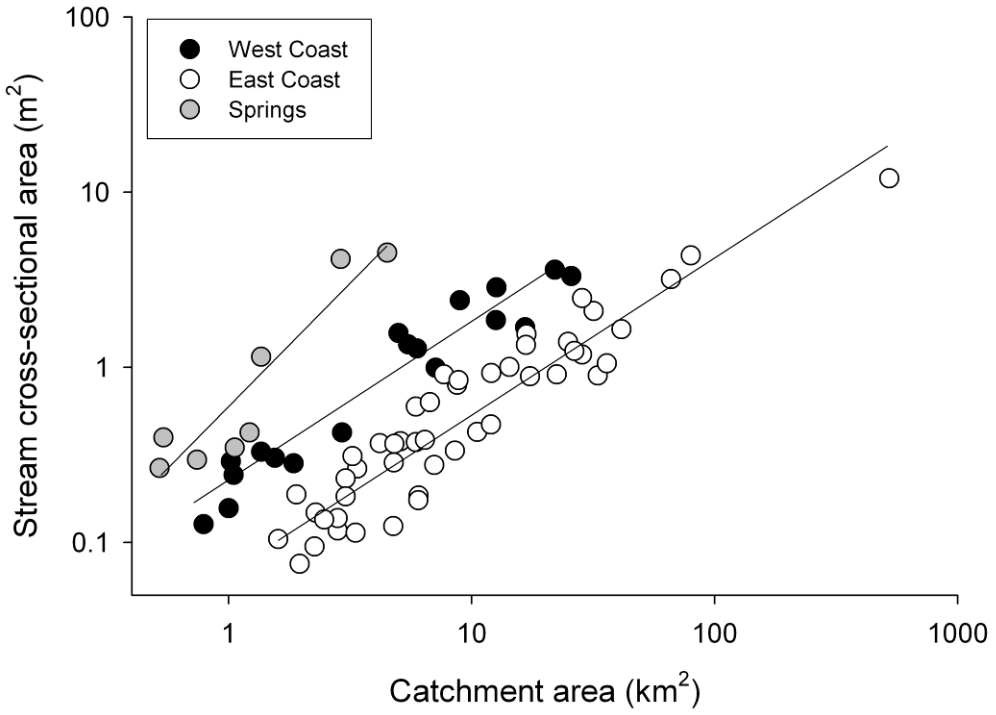
The impact of top predators in a changing climate

Perturbations that reduce habitat size (often modelled as river discharge) for fishes in lotic systems are predicted to increase under climate change scenarios due to reduced precipitation (because of warming temperatures) and increased water abstraction (Vörösmarty et al. 2000, Xenopoulos et al. 2005, Xenopoulos & Lodge 2006). Climate change models also suggest that declining river flows coupled with compensatory increases in water abstraction will cause many fish species to tend towards extinction and that the sizes of surviving fish species will be smaller (Xenopoulos et al. 2005, Xenopoulos & Lodge 2006, Daufresne et al. 2009). A decrease in the body size of top predators (i.e., towards smaller fishes) may have important implications for food-web structure and stability (McCann et al. 2005, Gotelli & Ellison 2006), because smaller body sizes will likely alter predation pressure and/or food availability for lower trophic levels resulting in potential trophic cascades (Casini et al. 2008, Andersen & Pedersen 2010).

At the individual level, body size strongly influences species interactions (Woodward et al. 2005). As the outcomes of such interactions are largely determined by body size, any alteration to body size distributions (and top predator body size) within communities will have important consequences for the wider food web (Woodward & Warren 2007). Woodward & Warren (2007) considered that body size distributions were determined by a combination of biotic and environmental factors whose relative importance varied with spatial scale, but noted that whilst shifts in taxonomic composition across abiotic gradients were well

known, a similar understanding of body size variation across environmental gradients was only available for marine systems. My study has shown that body size varies across multiple environmental gradients, and both survey and experimental work demonstrated that the major drivers of top predator body size were habitat size and disturbance. These results imply that the interaction between habitat size and disturbance largely controls top predator body size in these stream systems. Top predator effects on food webs are likely to vary with body size, therefore, the relationships found in this research should be incorporated into future models of food-web responses to shifts in habitat size and disturbance regimes with changing climate conditions.

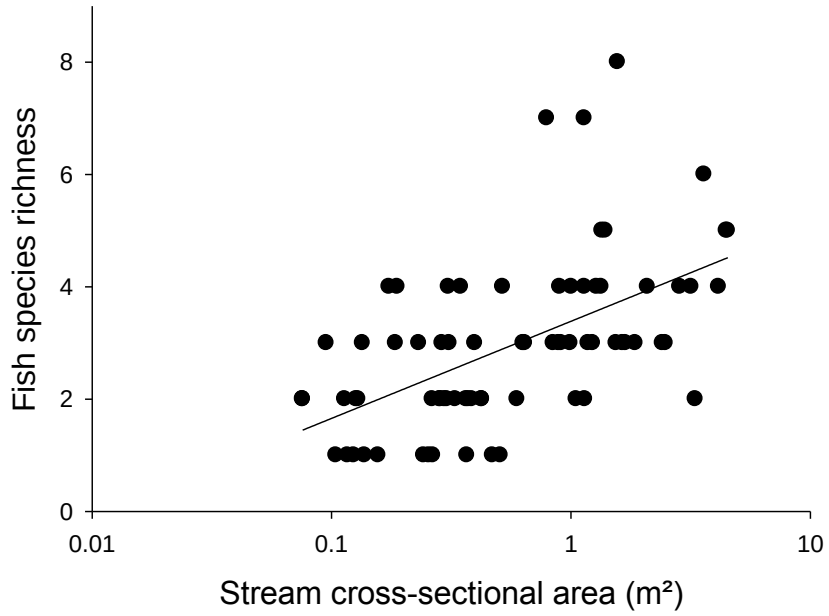
Appendices



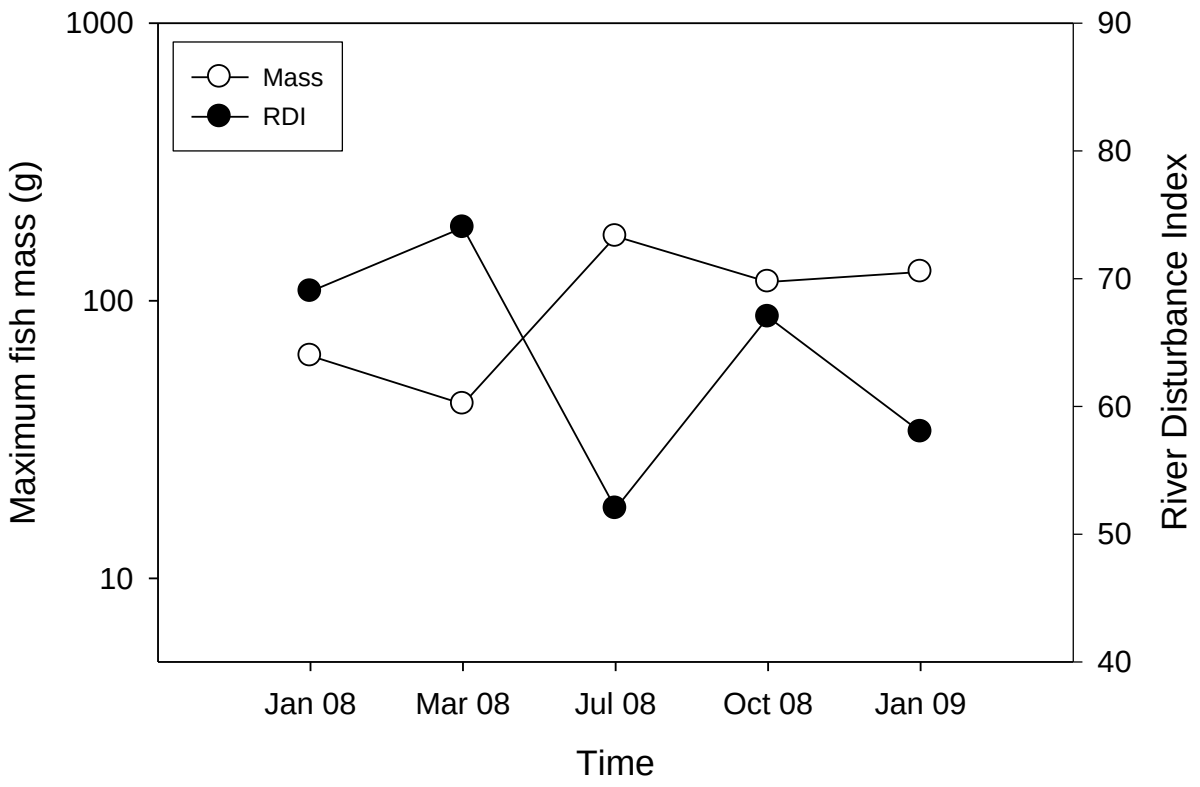
Appendix 1. Relationships between mean stream cross-sectional area and estimated catchment area (derived from digital elevation data in a GIS) for the 74 surface runoff-fed and spring-fed streams. For the three stream types, stream cross-sectional area and catchment area are tightly related. However, regression slopes or intercepts differ for each stream type (West Coast: $y = 0.21x^{0.92}$, $R^2 = 0.93$; East Coast: $y = 0.07x^{0.89}$, $R^2 = 0.87$; Springs: $y = 0.57x^{1.42}$, $R^2 = 0.86$), and is why stream cross-sectional area (rather than catchment area) is used to generalise habitat size across all waterways.

Appendix 2. Table of all fish species (common and scientific names given) that were caught during the survey. The number of sites and the location (East and/or West Coast) in which the fishes were captured is given, as well as disturbance scores and the size ranges of streams in which they found.

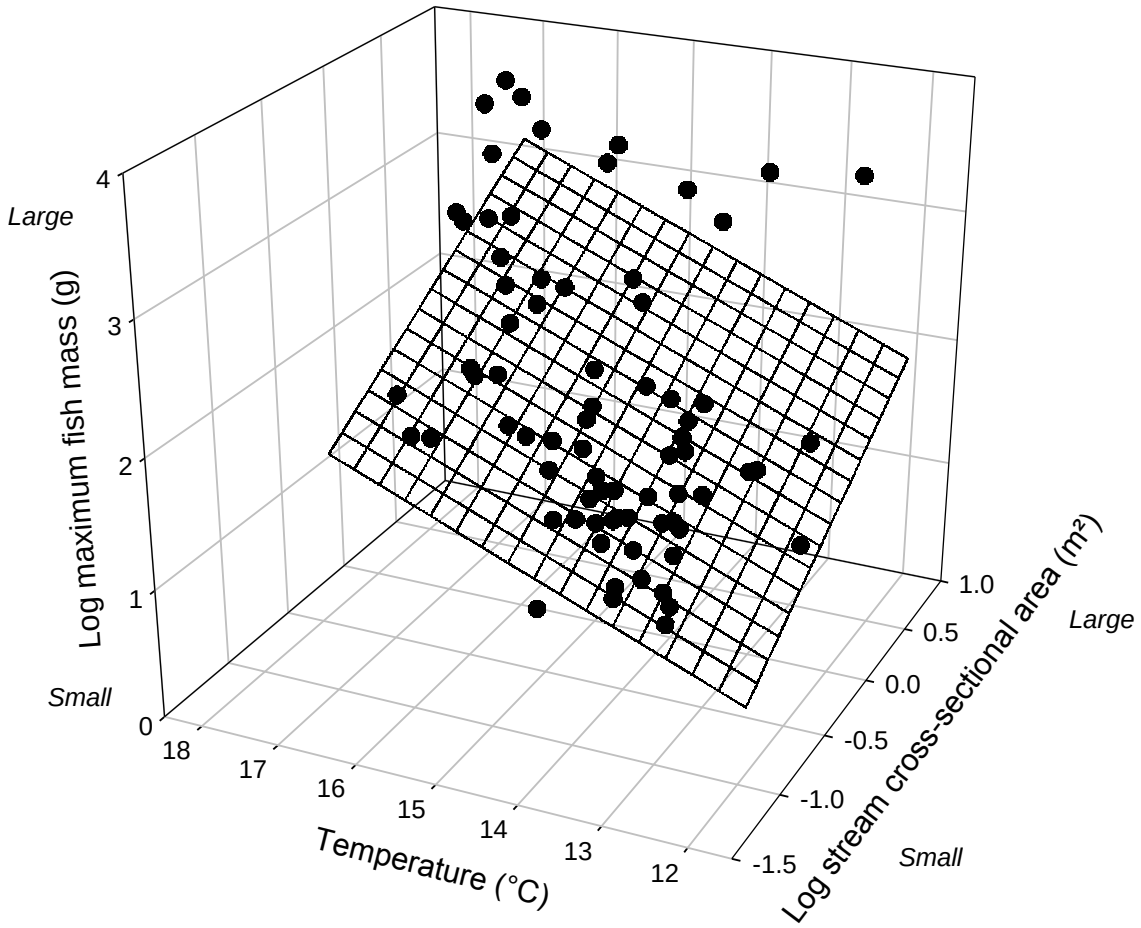
Fish species			Location	Stream size	RDI
Common name	Scientific name	*n*	(East/West)	range (m²)	scores
longfin eel	*Anguilla dieffenbachii*	44	East/West	0.08 – 4.52	46 – 111
shortfin eel	*Anguilla australis*	4	East/West	1.01 – 3.61	60 – 111
torrentfish	*Cheimarrichthys fosteri*	8	East/West	0.99 – 3.61	50 – 111
giant kokopu	*Galaxias argenteus*	3	West	1.28 – 2.86	59 – 72
banded kokopu	*Galaxias fasciatus*	8	East/West	0.16 – 2.86	64 – 109
shortjaw kokopu	*Galaxias postvectis*	4	West	1.14 – 1.57	59 – 109
koaro	*Galaxias brevipinnis*	10	East/West	0.10 – 1.69	54 – 109
inanga	*Galaxias maculatus*	1	West	3.61	111
Canterbury galaxias	*Galaxias vulgaris*	33	East	0.08 – 4.52	46 – 137
alpine galaxias	*Galaxias paucispondylus*	17	East	0.17 – 4.52	57 – 137
redfin bully	*Gobiomorphus huttoni*	9	East/West	0.91 – 3.61	50 – 111
common bully	*Gobiomorphus cotidianus*	4	West	1.28 – 1.86	55 – 72
bluegill bully	*Gobiomorphus hubbsi*	7	East/West	0.91 – 3.61	50 – 111
upland bully	*Gobiomorphus breviceps*	13	East/West	0.17 – 4.47	53 – 137
brown trout	*Salmo trutta*	30	East/West	0.13 – 4.52	47 – 137
rainbow trout	*Oncorhynchus mykiss*	17	East	0.10 – 3.18	53 – 141
Chinook salmon	*Oncorhynchus tshawytscha*	6	East	0.79 – 4.52	57 – 137



Appendix 3. The relationship between stream size and fish species richness ($y = 0.75 \ln x + 3.39$, $R^2 = 0.31$).



Appendix 4. A comparison of maximum fish mass (i.e., top predator body size) and disturbance over time at one of the sites used in the post-disturbance survey.



Appendix 5. Three-dimensional scatter plot with a fitted plane ($R^2 = 0.40$, $F_{2, 73} = 22.65$, $P < 0.0001$) to illustrate how the response of maximum fish mass (log maximum fish mass) changes across temperature and habitat-size (log stream cross-sectional area) axes.

Plate 8. Endangered giant kokopu (*Galaxias argenteus*) are occasionally found in forested streams (Photo credit: Angus McIntosh).

Chapter Five

Habitat size and external prey subsidies drive changes in stream food-web structure

Abstract

Land-use intensification and habitat fragmentation are causing widespread habitat loss. Changes in habitat size are impacting ecological communities, particularly predator populations, and are also disrupting the flow of resources across ecosystem boundaries (e.g., a decoupling of stream habitats from riparian vegetation). Predicting the consequences of habitat contraction and other global changes is limited by poor understanding of how complex food webs are structured in space and time. To measure changes to food-web structure, I constructed Eltonian biomass pyramids from stream communities across a gradient of habitat size to evaluate variation in predator biomass relative to prey biomass. The influence of external resource subsidies (e.g., terrestrial insects) was tested by assessing changes to food-web structure in grassland versus forested streams. Food webs became increasingly inverted in larger habitats (i.e., more predator than prey biomass) in both stream types, with similar rates of change in food-web structure with habitat size in the two stream types. However, significantly more terrestrial prey items were present in the drift at forested streams, and this additional prey subsidy was likely responsible for there being consistently more predator biomass (per unit of prey biomass) supported in forested compared to grassland streams. In addition to external prey subsidies, high prey turnover rates, low predator turnover and spatial coupling of prey resources by predators likely explained why increasingly inverted biomass pyramids occurred as habitats became larger. These mechanisms and patterns, along with increases in predator richness and evenness with habitat size suggested that inverted biomass pyramids were more likely to occur in large habitats because larger habitats allowed these

structures to be stable. These findings indicate that a habitat's capacity to support predator biomass changes with habitat size and that land-use changes causing habitat decoupling or habitat compression will result in habitats with a reduced capacity to support predator biomass.

Introduction

Across all ecosystems, humans are impacting ecological communities (Walther et al. 2002, Didham et al. 2007), particularly species at the top of food webs (Pauly et al. 1998, Olsen et al. 2004, Darimont et al. 2009). Habitat loss through land-use intensification and habitat fragmentation has resulted in unprecedented declines in top predators (Duffy 2003), and climate warming is predicted to further increase extinction rates at higher trophic levels (Petchey et al. 1999, Voigt et al. 2003). The ecological consequences of predator loss on food webs is poorly understood (Banavar & Maritan 2009), mainly because studies have focussed on species loss at lower trophic levels (Hooper & Vitousek 1997, Tilman et al. 2001). Predator diversity can enhance food-web complexity, reduce interaction strength and increase the likelihood of omnivory (McCann & Hastings 1997, Finke & Denno 2004, McCann et al. 2005), so predator loss may have far-reaching implications for the structure and functioning of food webs (Borvall & Ebenman 2006). Predator loss is often coupled with reductions in habitat size (Srivastava et al. 2008), so a better understanding of the relationship between predator abundance and habitat size is required.

Habitat size can influence predator size, composition and abundance (Harestad & Bunnel 1979, Minns 1995), so predator loss may be closely linked to the capacity of habitats to support particular types of predators. Habitat reduction experiments in terrestrial ecosystems indicate that habitats quickly lose their large top predators as they become smaller (Diamond 2001). The construction of a dam in Venezuela which flooded a valley turning

former hilltops into a series of islands (0.1 to 150 ha), for example, led to top predator loss from all islands (i.e., the jaguar, puma and harpy eagle) within four years (Diamond 2001, Terborgh et al. 2001). To date, few studies have attempted to evaluate how changes in habitat size affect a system's capacity to support predators. A reduction in habitat size should negatively impact species diversity and other food-web properties such as food chain length, interaction strength and body size (MacArthur & Wilson 1967, Spencer & Warren 1996, Vander Zanden et al. 1999, Post et al. 2000, Post 2002, McCann et al. 2005), which may affect predator abundance/identity, and food-web structure and stability (Polis & Strong 1996, Post 2002).

Food-web structure is likely to vary spatiotemporally with habitat size, and this shift in structure can be quantified through food-web shape (e.g., trophic pyramids, Elton 1927). Eltonian biomass pyramids graphically depict the distribution of biomass across trophic levels, and can summarise shifts in food-web structure such as changes in the proportion of predator biomass relative to prey biomass. Predator-prey biomass ratios, which measure pyramid shape, are often used to show food-web responses in body size and allometric models (e.g., Kruger & McGavin 2001, Donald & Anderson 2003), but they have only recently been used to assess community-level variation in food webs (e.g., Thompson & Townsend 2005).

Typical terrestrial biomass pyramids have a large biomass of prey supporting a smaller biomass of predators, but inverted biomass pyramids, with more predator than prey biomass, are more common in aquatic systems (e.g., lakes, marine coral reefs) (Odum 1971, Del Giorgia et al. 1999, Sandin et al. 2008). The distinction between biomass and productivity (energy flux) pyramids is important because productivity is constrained by thermodynamic laws requiring that energy flux be greater at lower trophic levels compared to higher levels, so unlike biomass pyramids, productivity pyramids can never be inverted (Ballantyne 2004,

Brown et al. 2004). Thus, to get an inverted biomass pyramid, productivity must still be higher at lower trophic levels. Multiple hypotheses including high prey turnover rates (Odum 1971), low predator turnover (Del Giorgia et al. 1999), spatial coupling of prey by predators (McCann et al. 2005) and predator subsidisation by an additional prey source (Wang et al. 2008) may explain the persistence of inverted biomass pyramids. These hypotheses are not mutually exclusive, as all four mechanisms may contribute to inverted biomass pyramids being supported.

Some theory suggests inverted biomass pyramids should be unstable food-web structures (Neutel et al. 2002), yet empirical observations from different aquatic ecosystems shows that these types of food webs persist over time (e.g., Huryn 1998) and across space (e.g., Del Giorgia et al. 1999). Food webs in small habitats may have different food-web structures and dynamics compared to larger habitats due to increases in the strength of predatory interactions in spatially compressed food webs (McCann et al. 2005). However, a change in food-web structure with habitat size does not necessarily imply a change in food-web stability because different mechanisms may operate to maintain the stability of contrasting food-web structures (i.e., standard versus inverted biomass pyramids) across different sized habitats. Empirical studies assessing variation in food-web structure over environmental gradients (e.g., habitat size) are lacking, and consequently, our ability to predict how predators may respond to changes in habitat size is limited.

Defining realistic habitat boundaries so that habitat size can be measured empirically is difficult because studies of cross-ecosystem interactions indicate substantial linkages between ecosystems (e.g., Polis et al. 1997, Huxel & McCann 1998, Baxter et al. 2005, Greenwood & McIntosh 2008). Food-web studies at the interface of contrasting ecosystems (e.g., terrestrial and aquatic) indicate reciprocal resource subsidisation occurs, allowing increased predator populations to be supported (Nakano & Murakami 2001). Thus, predator

subsidisation by additional prey sources may explain the presence of inverted biomass pyramids (e.g., Wang et al. 2008). However, the importance of subsidies to recipient food webs may vary with habitat size. For example, the relative contribution of terrestrial energy from forested habitats to stream food webs may decrease as streams become larger (Vannote et al. 1980). Thus, understanding of habitat size-dependent variation in the propensity of food webs to support predator biomass could be enhanced by studying habitat size-related variations in resource subsidies.

To investigate variation in food-web structure in response to changes in habitat size, I measured changes in the ratio of predator biomass to prey biomass across three orders of magnitude in stream size. The influence of external resource subsidies (i.e., terrestrial prey subsidies) on food webs was tested by assessing food-web structure in grassland compared to forested streams (i.e., contrasting stream types), since forested streams should have higher terrestrial inputs than grassland streams. Therefore, I hypothesised that for a given habitat size, forested streams would support more predator biomass than grassland streams, and that this additional predator biomass would result in forested streams having inverted biomass pyramids across the habitat size gradient.

Methods

Study Area

Stream food webs and physical attributes were sampled at 43 streams in four regions of New Zealand (see Fig. 1). Thirty-eight streams in three regions of the South Island (Banks Peninsula, Canterbury high country and Westland) were sampled from 2004 – 2009, and five streams were sampled in the Coromandel, North Island from 1996 – 1998 (data supplied by

D.W. West, see West et al. 2005). Selected streams fell into two categories based on the riparian vegetation type present: (i) grassland (25 streams) and (ii) forested (18 streams). In practice, this meant that for at least 1000 m upstream of the sampling reach the specified riparian vegetation type was present. Grassland stream vegetation was composed of either low tussock grasses (*Festuca* sp. and *Poa* sp.) or a mixture of tussock and exotic pasture grasses; both grassland vegetation types were subject to low intensity grazing. Forested streams were located in native forest (although forest type varied greatly with location), and all forested streams had greater than 80% overhead cover with the exception of the two largest forested sites.

Within grassland and forested catchments, second to fourth-order streams were selected that encompassed a broad range of stream size (grassland: 0.8 – 11.6 m wide, forested: 0.5 – 11.7 m wide) and disturbance (stream stability). At each site, a single-thread 50 m survey reach was selected which was wadeable and less than 15 m wide (so it could be quantitatively electrofished). A 25 m section of the reach was used for electrofishing, and this section would always include all habitat types present (e.g., pool, riffle, run). Sites were excluded if they: did not meet these criteria, were fishless, had pH values that may prohibit some fish species from being present (< 6 or > 8.5) or had high conductivity values (> 150 $\mu S \cdot cm^{-1}$; indicative of potential water pollution in these particular catchments).

Habitat surveys

Habitat size was defined as stream cross-sectional area (m^2) and was calculated by averaging the two-dimensional area of five width-depth transects over a 50 m reach measured on multiple occasions (3–7 depending on location) at each study site. Width transects were located at 10 m intervals and at least five depth measurements were made at equally spaced intervals across each transect. Catchment area was not used as a measure of habitat size

because the relationship between stream size and catchment area can vary regionally and with flow source (e.g., surface-runoff or spring-fed) (see Chapter 4). Water temperature as well as a range of water chemistry measures including pH, conductivity and dissolved oxygen was also measured at each site with hand-held meters (pH and dissolved oxygen data were not available for the five Coromandel streams).

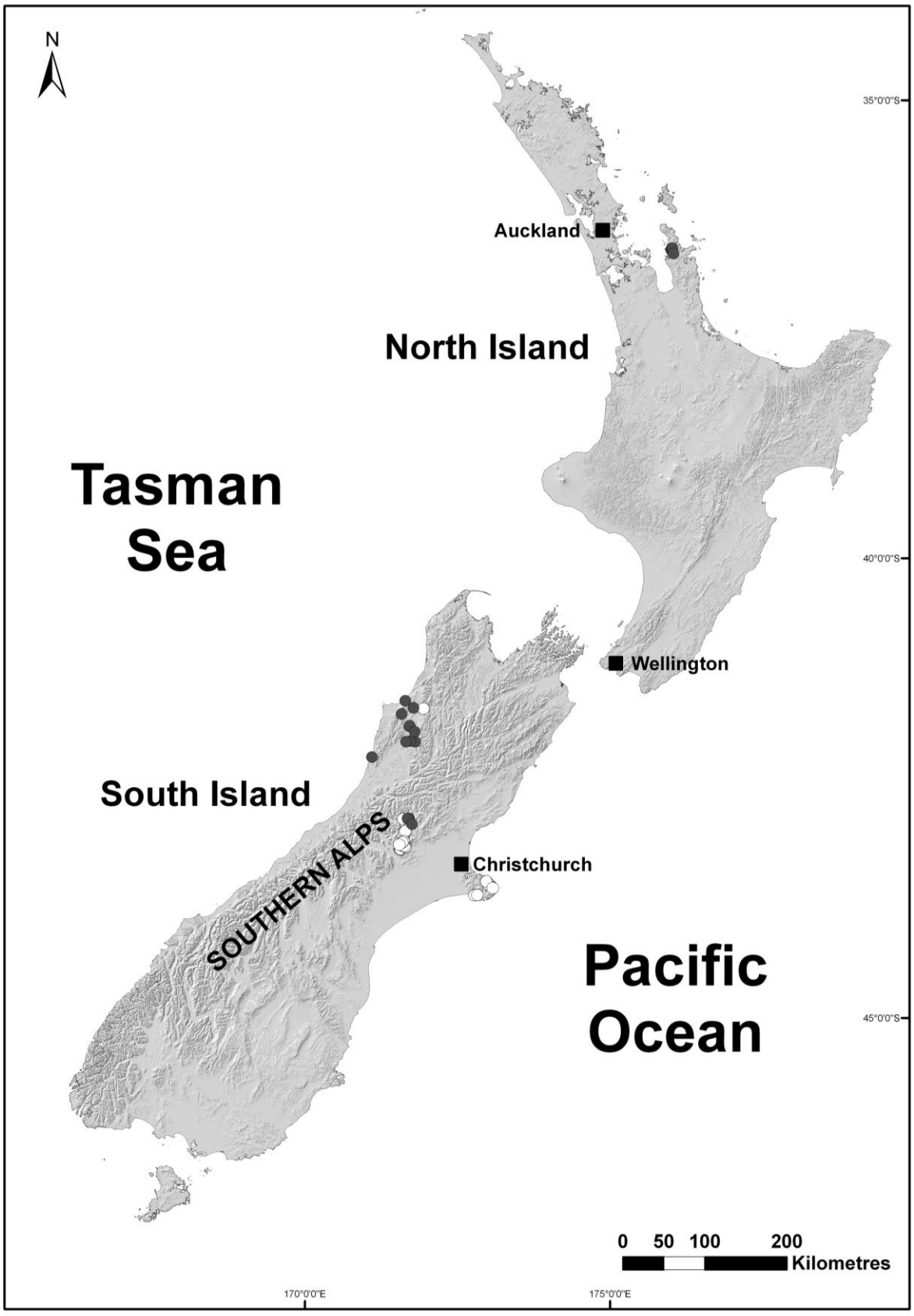


Figure 1. The distribution of streams sampled across New Zealand. White circles indicate grassland sites and solid circles indicate forested sites.

Disturbance was assessed using a subjective river disturbance index (hereafter abbreviated to RDI) (Pfankuch 1975) based on 15 categories that evaluate landscape, riparian and stream characteristics. The observer visually grades each category and the scores are summed to give an overall index score (RDI range: 38–152) which indicate whether the waterway is stable (small number) or physically unstable/highly disturbed (large number). This index correlates strongly with other disturbance measures such as multivariate and bed disturbance indices (e.g., Death & Winterbourn 1994, Townsend et al. 1997b, Chapter 1).

Sampling stream food webs

Benthic stream invertebrates (i.e., prey) and fishes (i.e., predators) were sampled at all streams, with all benthic invertebrates considered prey because all invertebrate species including predatory invertebrates have been found during stomach content analyses of predatory fishes (e.g., large megalopteran larvae in the stomach of brown trout) (McHugh et al. 2010). To characterise prey richness and biomass, five Surber samples (0.0625 m^2, mesh size 250 µm) were taken in random riffle or run habitat every 10 m within the 50 m sampling reach. Samples were preserved in 90% ethanol, and then sorted and identified in the laboratory at a magnification of ×10. Aquatic invertebrates were identified to either genus or species level (except Chironomidae, which were identified to sub-family) using the keys of Winterbourn et al. (2000). Prey weight was determined using two methods. For 18 grassland sites, all invertebrates were counted in each sample, then a random subset of individuals for each species was measured (up to 50 individuals per site), and then length-weight regressions (Towers et al. 1994) were used to determine invertebrate dry weight. Processing invertebrates using this technique allowed both biomass and body size data to be collected although invertebrate body size data are not presented in this chapter. The dry weight of benthic invertebrates at the remaining 25 sites was calculated by air drying for at least 48 h at 50 °C,

then weighing samples to the nearest 0.1 mg on a Mettler Toledo AB204-S balance (Küsnacht, Switzerland). To ensure accurate dry weights were obtained, all caddisfly larvae were removed by hand from their cases, and all snails were placed in 10% HCl solution to dissolve their shells.

To determine predator richness and biomass, stream fish communities were measured by electrofishing at least 25 m (and up to 75 m depending on size) of the sampling reach. The sampling reach was quantitatively three-pass electrofished with stop nets in place. All streams were surveyed using a Kainga EFM 300 backpack electrofishing machine (NIWA Instrument Systems, Christchurch, N.Z.) with 300 – 600 V pulsed DC (pulse width ~ 3 ms, 60 pulses s^{-1}), and with the operator moving in a downstream direction towards a 1 m wide push net (mesh size 3 × 2 mm ellipse). Electrofishing in a downstream direction is the most efficient method for capturing fish species in these streams (Jellyman & McIntosh 2010). All captured fishes were anaesthetized with 2-phenoxyethanol, measured [to the nearest 1 mm; fork length (FL) for salmonids and total length (TL) for other species], weighed and released. Fish densities were calculated using the maximum likelihood equations for three-pass depletion sampling (Cowx 1983).

Stream drift was quantified in a subset of the 43 streams (17 grassland and 17 forested) to measure the amount of aquatic and terrestrial prey available to predatory fishes in the two stream types. Invertebrate drift was measured with two nets (30 × 25 cm front opening, 1 m long, 200 µm mesh) deployed for approximately two hours during the day (starting 0930 hours) and night (starting 2100 hours) at each site. In streams where the water depth was greater than the drift net height, nets were purposely set so that they could capture invertebrates floating on the stream surface and the cross-sectional area filtered was measured. Water velocity through the nets was measured using a current meter (Marsh-McBirney Flo-Mate® Model 2000, Frederick, MD, U.S.A.) at the start and finish of drift

sampling to calculate the volume of water each net had filtered. Aquatic and terrestrial invertebrates were separated during processing, and the weight (ash-free dry mass, AFDM) of both prey groups was calculated by air drying for at least 48 h at 50 °C, followed by ashing at 550 °C for 4 h. Invertebrate drift was calculated as drift density, and expressed as numbers per m^{-3} of water filtered.

Data analysis

Patterns in food-web structure and resources

To examine whether the food-web structure measured by predator-prey biomass ratios altered with stream size and whether the patterns in grassland streams were different to forested streams, a homogeneity of slopes test was performed with stream type as the covariate, habitat size as the continuous predictor and a stream type by habitat size interaction. A non-significant interaction term in the homogeneity of slopes test was followed by analysis of covariance (ANCOVA) with stream type and habitat size as the main effects.

The availability of additional prey resources (i.e., terrestrial invertebrates) to predatory fishes in grassland and forested streams was investigated by analysing drift samples. The contribution of terrestrial invertebrates to the total weight of drift samples was determined for each site so the proportion of drift weight from terrestrial invertebrates could be compared between stream types using one-way ANOVA.

Evaluating mechanisms influencing food-web structure and stability

In addition to investigating changes in food-web structure with stream size and the influence of external resource subsidies, *post hoc* analyses were conducted to evaluate mechanism(s) that might explain variation in food-web structure and stability. I evaluated whether changes in food-web structure across the habitat size gradient (for grassland and forested streams)

were due to: (1) the addition of predatory fish species, (2) variation in the evenness of predatory fish communities (i.e., a change in single-species dominance), (3) a change in predator density, or (4) a shift in mean predator body size. To investigate (1), I tested how predator richness (relative to prey richness) varied with habitat size. Given that different predatory fishes may dominate in particular environmental conditions (see Chapter 3), I assessed variation in the evenness of predatory fish assemblages across the habitat size gradient (2). If environmental conditions remain relatively constant, a change in predatory fish biomass per unit area requires that either predator density or mean predator body size (per unit area) also changes. To address (3) and (4), I tested for relationships between predator density and body size and habitat size. For all regression-based analyses, biomass data were log-transformed prior to statistical tests in the R software package (R Development Core Team 2009).

Results

Survey overview

The 43 streams used to evaluate changes in food-web structure encompassed a wide gradient of habitat size [(grassland mean (range): 1.05 m^2 (0.12 – 4.1), forested mean (range): 0.72 m^2 (0.06 – 3.6)] and disturbance [(grassland mean (range): 86 (50 – 124), forested mean (range): 83 (56 – 111)]. An orthogonal dataset was assembled in which neither habitat size nor disturbance were correlated (both stream types: $R^2 < 0.13$, $P > 0.05$), thus, variation due to disturbance did not confound analyses. There was some variation in the range of species richness values between stream types but mean richness was very similar. Species richness varied in the grassland sites from 1 – 5 predatory fish species (mean: 2.9) and 15 – 33 (mean:

23.1) prey taxa, whereas forested streams contained 1 – 9 fish species (mean: 2.8) and 14 – 38 (mean: 24.3) invertebrate taxa.

Patterns in food-web structure and resources

Habitat size explained 46% and 58% of the variation (R^2) in food-web structure in grassland and forested streams, respectively (grassland: $F_{1, 24} = 19.42$, $P < 0.001$; forested: $F_{1, 17} = 21.99$, $P < 0.001$) (Fig. 2). In grassland streams, the predator to prey biomass ratio increased from less than 0.3 in the smallest sites to over 10 in the largest sites. Thus, biomass pyramids in grassland streams changed from having a standard pyramid shape in small streams to having inverted pyramids in large streams. In contrast, biomass pyramids in forested streams were inverted even in small habitats, although they also became increasingly inverted as streams got larger.

The regression slopes in grassland and forested streams were homogeneous (habitat size × stream type: $F_{1, 39} = 0.18$, $P = 0.68$) indicating that the rate of change in food-web structure (i.e., the change in the predator: prey biomass ratio) with habitat size was similar between stream types. ANCOVA showed that the regression intercept for forested streams was significant higher than the intercept for grassland streams (stream type effect: $F_{1, 40} = 188.81$, $P < 0.001$). This indicated that for a given stream size, forested streams were able to support more predator biomass (per unit of aquatic prey biomass) than grassland streams.

To examine why forested streams were supporting more predator biomass than grassland streams of similar sizes and aquatic prey biomass, drift samples were analysed. A comparison of the proportion of terrestrial biomass in drift samples showed that at forested sites, the proportion of terrestrial invertebrate biomass in drift samples was significantly higher than at grassland sites (one-way ANOVA: $F_{1, 33} = 70.50$, $P < 0.001$) (Fig. 3). Drift samples at forested sites had almost four times more terrestrial invertebrate biomass than

those in grassland sites. Regression analysis showed that the proportion of terrestrial biomass in these drift samples did not significantly vary over the habitat size gradient in either stream type (both stream types: $R^2 < 0.12$, $P > 0.05$), although clearly, forested streams were receiving a substantial terrestrial prey subsidy compared to grassland streams.

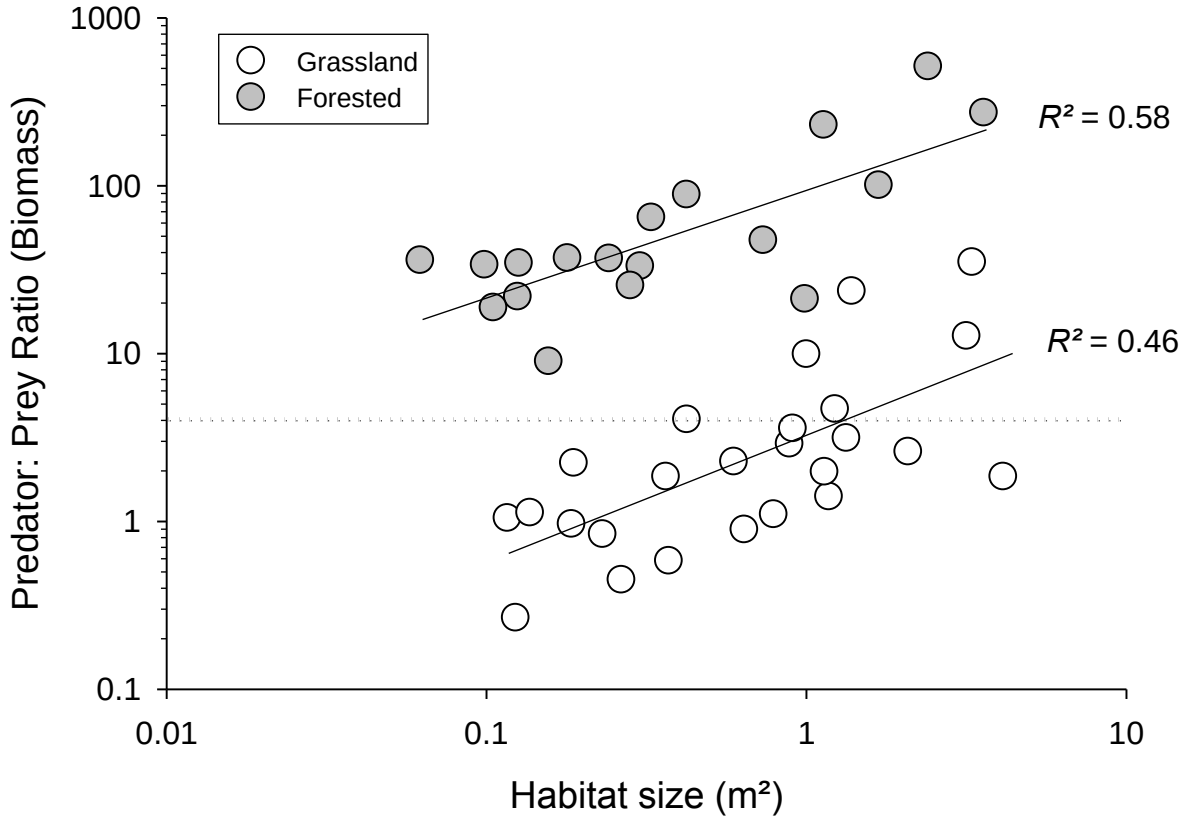


Figure 2. Change in the ratio of predator biomass to prey biomass across the habitat size gradient at grassland and forested sites. The dotted line represents a change in food-web structure, below this line food webs are pyramid shaped but above this line food webs become inverted (this line is set at a ratio of 4 to make a standardised comparison between predator and prey biomass because predator dry weights are approximately 25 % of their wet weight; P. Jellyman *unpubl. data*). Regression equations are $y = 3.07x^{0.75}$ and $y = 96.08x^{0.66}$ for grassland and forested streams, respectively.

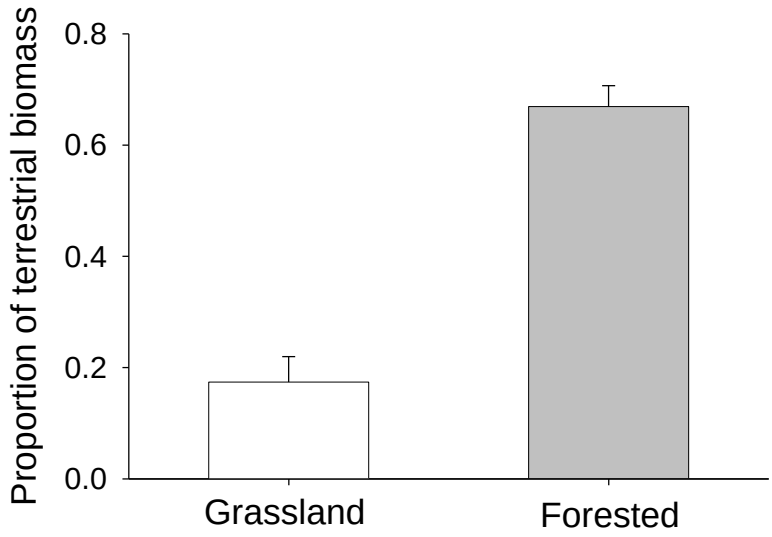


Figure 3. The mean (+SE) proportion of prey biomass in drift samples that was of terrestrial origin at grassland and forested sites. Terrestrial invertebrates were measured in grams of AFDM and biomass was calculated by determining the g AFDM per m^3 of water filtered through the drift nets at each site.

Evaluating mechanisms influencing food-web structure and stability

There was a strong contrast in the quantity of predator and prey biomass that structured food webs in each stream type. On average across all stream sizes, grassland streams supported slightly more predator than prey biomass ($F_{1, 49} = 6.68$, $P = 0.01$, Fig. 4a), whereas in forested streams, there was twelve times more predator than prey biomass ($F_{1, 35} = 9.95$, $P < 0.001$, Fig. 4b). In grassland streams, prey biomass was consistently about 5 $g \cdot m^{-2}$ in all streams, whereas predator biomass significantly increased across the habitat size gradient (Figs. 4c, e). In contrast, predator biomass did not significantly change with habitat size in forested streams, but prey biomass declined by about two orders of magnitude as stream size increased (Figs. 4d, f).

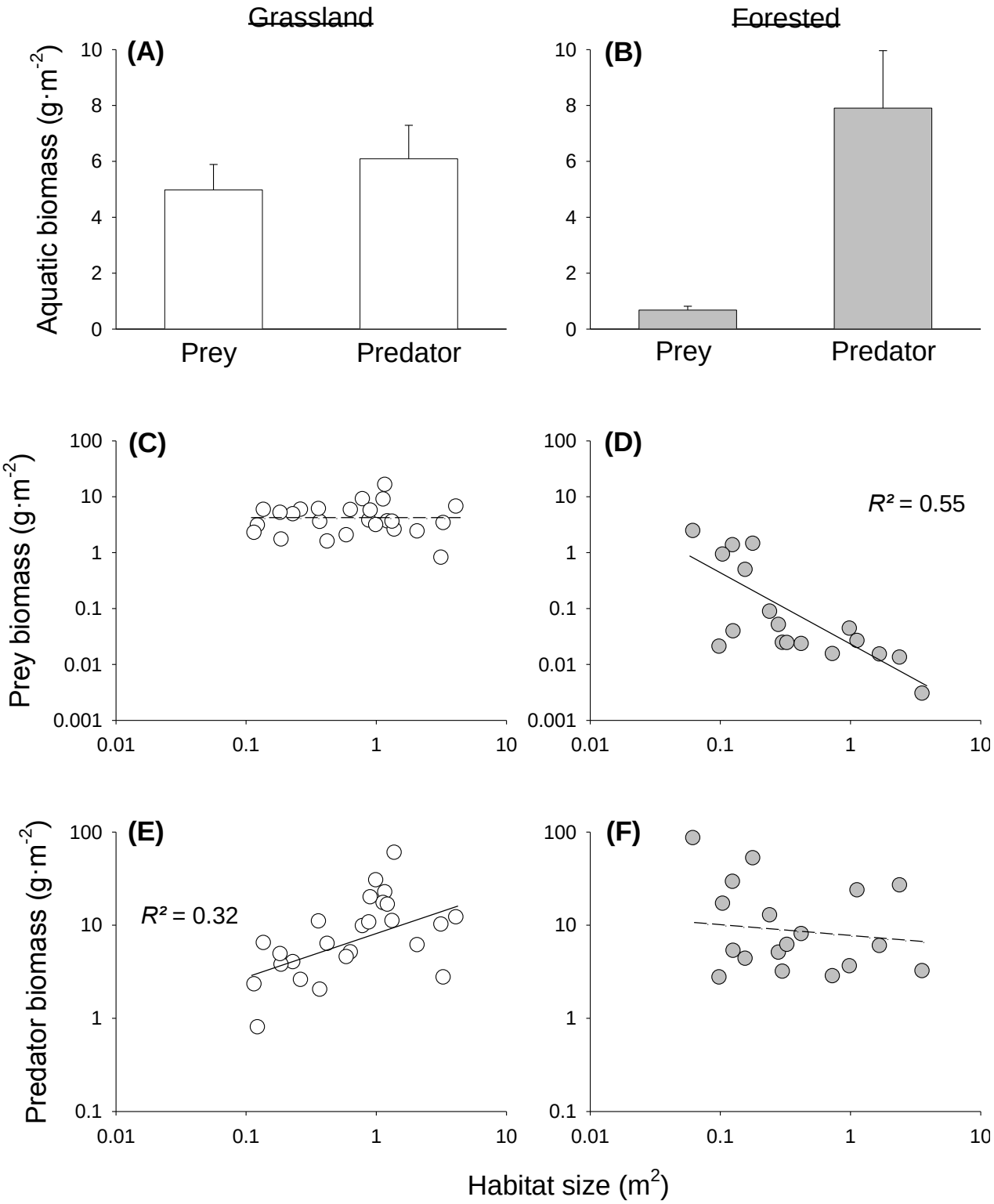


Figure 4. Changes in aquatic prey and predator biomass at grassland and forested sites. Figures show the mean (+SE) biomass at grassland and forested sites (a-b), and patterns in biomass of prey and predators across the habitat size gradient (c-f). Significant regressions are shown as solid lines and dashed lines represent non-significant regressions. Note, prey was measured as grams of dry weight but predators as grams of wet weight.

In addition to food-web structure, a number of mechanisms linked to food-web stability were also investigated. An analysis of species richness across the habitat size gradient showed that as grassland and forested streams got larger, there was a significant increase in the number of predator species relative to prey species present (Figs. 5a, b). In small grassland and forested streams, there was approximately one predator to fifteen prey species compared to the largest streams where there was one predator for every four to five prey species. For both stream types, this change in the species richness ratio was largely driven by increases in predator richness with habitat size (grassland: $R^2 = 0.41$, $F_{1, 24} = 16.11$, $P < 0.001$; forested: $R^2 = 0.34$, $F_{1, 17} = 8.38$, $P = 0.01$). A significant increase in predator species evenness in both stream types (Figs. 5c, d) was also associated with the addition of new predator species as habitats became larger. This indicated that single species dominance of the food web was lessened with increasing habitat size. In grassland streams, increasing species evenness occurred across the habitat size gradient despite an increase in predator body size (Fig. 5e).

As previously described, predator biomass increased as grassland streams became larger, whereas in forested streams, predator biomass remained relatively constant (Figs 2e, f). The increase in predator biomass in grassland streams was due to an increase in mean predator size (which increased from 5 to 58 g, Fig. 5e) because predator density did not change across the habitat size gradient ($R^2 < 0.04$). Predator body size was consistently about 40 g across the habitat size gradient in forested streams (Fig. 5f), and since predator density did not significantly change with habitat size in forested streams either ($R^2 < 0.03$), neither did predator biomass.

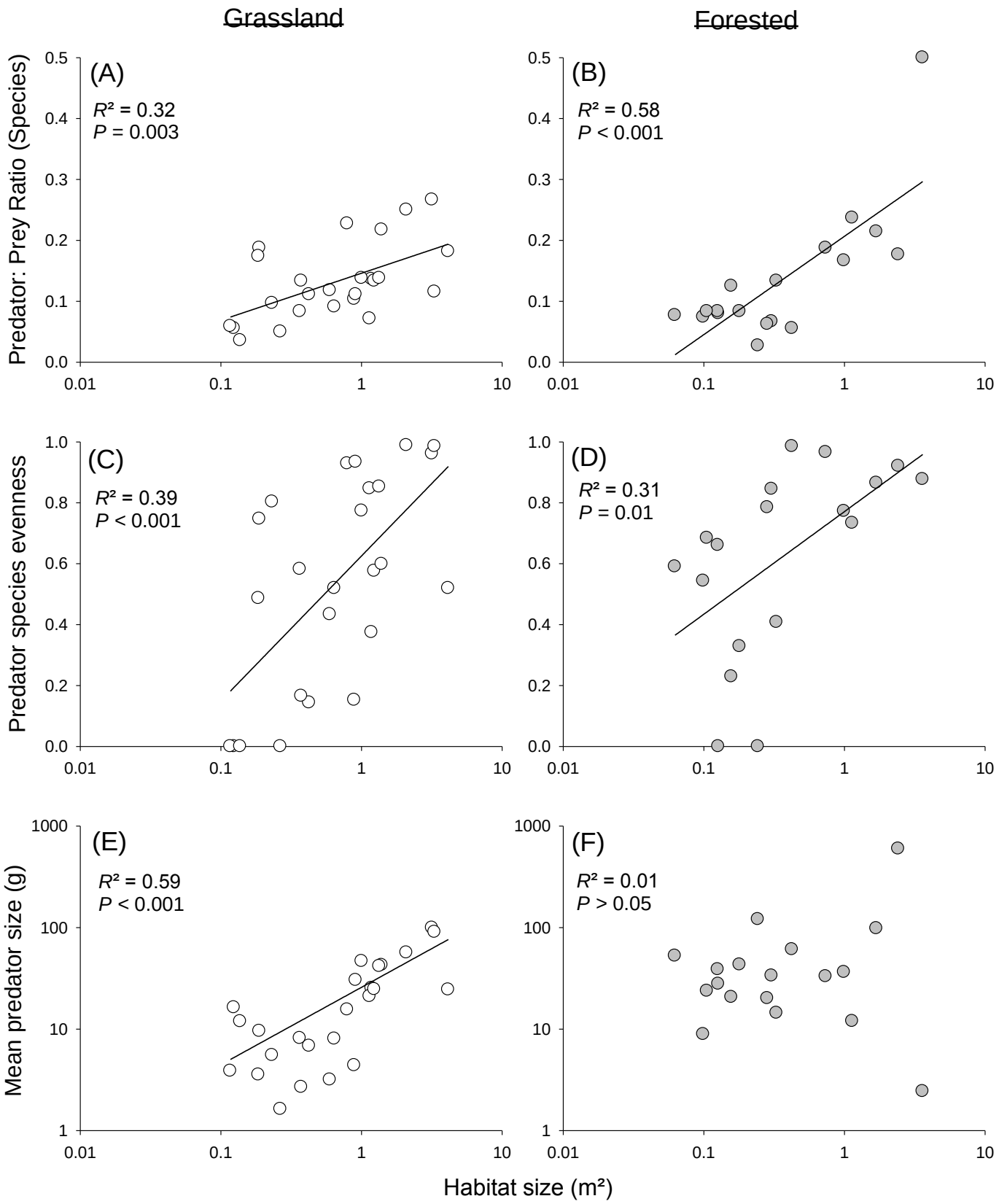


Figure 5. Relationships between habitat size and proximate mechanisms (i.e., predator: prey species richness, predator species evenness and mean predator body size) influencing food-web structure in grassland (a, c, e) and forested (b, d, f) streams. Only significant regressions are shown.

Discussion

As ecological communities become increasingly influenced by global change phenomena such as land-use intensification, habitat fragmentation, climate warming and biotic invasion, being able to predict how 'at risk' predator communities will respond is critically important (Tylianakis et al. 2008). My research indicates that a food web's capacity to support predator biomass is likely to be altered by changes in habitat size and resource subsidies. Below I evaluate the likely causes of these patterns and discuss why inverted biomass pyramids may be a relatively common feature of large stream habitats. The results have significant implications for understanding and predicting food-web responses to global environmental change, so I conclude by discussing how the management of food webs in at risk habitats should be altered.

I found that habitat size and forested riparian stream margins explained the greatest variation in food-web structure. The relationship with habitat size was expected since previous studies have shown habitat size (also termed ecosystem size) is a fundamental determinant of a range of food-web properties including food-chain length, body size and interaction strength (Post 2000, McCann et al. 2005, Sabo et al. 2009). However, studies assessing changes in food-web structure across habitat size gradients are rare, and finding such a consistent change in food-web structure with habitat size in contrasting stream types was unexpected. In both grassland and forested streams, more predator biomass was supported relative to prey biomass as habitats became larger, resulting in increasingly inverted biomass pyramids in both habitat types.

Although the rate of change in food-web structure with habitat size was similar between stream types, more predator biomass was supported for any given habitat size in forested compared to grassland streams. Interestingly, the patterns were being driven by different responses of predator and prey biomass to habitat size in the two stream community

types. In grassland streams, increasingly inverted biomass pyramids occurred because predator biomass increased with stream size whilst prey biomass remained constant, whereas in forested streams, predator biomass remained constant whilst prey biomass decreased with increasing habitat size. These contrasting community responses meant that for any given stream size, forested streams were supporting 10 times more predator biomass per unit area than grassland streams. It is difficult to see how higher prey turnover rates in forested compared to grassland streams could explain how an order of magnitude more predator biomass was supported in forested streams. Moreover, primary and secondary production in forested streams is typically lower than in grassland streams because of shading (Huryn & Wallace 2000). Thus, the high proportion of terrestrial biomass in stream drift was almost certainly the additional prey source subsidising these predators. Terrestrial invertebrates comprise up to 89% of the diet of some predatory fishes in these forested streams (e.g., banded kokopu, West et al. 2005), and terrestrial prey subsidies are known to play a significant role in maintaining predatory fish populations in other forested stream ecosystems (Nakano et al. 1999, Nakano & Murakami 2001, Baxter et al. 2005).

Mechanisms for inverted biomass pyramids

Inverted biomass pyramids are found in many types of aquatic habitat including lakes, oceans and streams (Del Giorgia et al. 1999, Sandin et al. 2008, this study), but the relative importance of the four mechanisms so far proposed for their existence (i.e., high prey turnover, low predator turnover, predator movement coupling prey sources and additional prey subsidies) will likely vary between ecosystems. For example, in my streams, many predatory fish species have fixed territories and move less than 100 m in a typical year (Cadwallader 1976, Jellyman & Sykes 2003, West et al. 2005, Hansen & Closs 2009), so spatial prey coupling by predators may be more important in ocean or lake ecosystems

compared to streams. However, the higher amount of predator biomass supported in forested streams relative to grassland streams highlights the possible spatial coupling of streams to adjacent terrestrial environments, signalling that additional prey subsidies are more likely to influence stream ecosystems than lake or ocean ecosystems. High prey turnover rates are also important in sustaining predator biomass in most aquatic ecosystems, including grassland streams (Huryn 1998), coral reefs (Sandin et al. 2008) and lakes (Odum 1971), so prey turnover should be an important mechanism for sustaining most inverted biomass pyramids. In fact it could be that habitat size-dependent reductions in prey turnover or production underpinned the changes in prey biomass with habitat size in forested streams. As forested streams are heavily shaded (i.e., have low algal growth compared to grassland streams) they are reliant on terrestrial detrital inputs for energy (Wallace et al. 1997, 1999). However, as stream size increases, the ratio of overhanging riparian vegetation (and also terrestrial inputs) to stream width decreases. Thus, prey abundance may decrease with stream size until the canopy is sufficiently open enough for algal growth.

Low predator turnover rates are likely to be the most general mechanism producing inverted biomass pyramids. Long-lived predators are often observed in aquatic ecosystems (e.g., great white sharks > 35 years, Smith et al. 1998; longfin eels > 100 years, Jellyman 1995) and these predators are able to store the largest proportion of total energy in the food web (Ballantyne 2004). Low predator turnover can therefore result in high predator biomass (the fundamental property of an inverted biomass pyramid), particularly in large habitats.

In spatially expansive habitats (e.g., lakes or oceans), predators should strongly couple resources in space (potentially resulting in inverted biomass pyramids), whereas in spatially compressed systems, the spatial coupling effect of predators may be weak due to strong predator-prey interactions (McCann et al. 2005). The argument that largely underpins this theory is that as habitats increase in size, predators must couple prey resources over greater

spatial scales to increase their trophic position. The extent of prey coupling by predators is therefore largely determined by habitat size, suggesting that stronger prey coupling should occur in larger streams. A recent analysis of stream fish trophic position is in agreement with this suggestion, because trophic position increases with stream size (McHugh et al. 2010), indicating that predators in large streams are likely to be coupling resources over greater spatial scales than predators in small streams. Thus, in addition to spatial prey coupling by predators being a potential causal mechanism of inverted biomass pyramids, it may also explain why biomass pyramids become increasingly inverted as habitats get larger.

Connections between food-web structure and food-web stability

Empirical observations and ecological modelling agree that food webs can contain more predator biomass than prey biomass (i.e., maintain inverted biomass pyramids) and yet still have a stable food-web structure (Del Giorgia et al. 1999, Ballantyne 2004, Brown et al. 2004, Sandin et al. 2008). As a caveat to this, McCann et al. (2005) showed that predators could have a destabilising effect on food webs in smaller habitats because predators can exert strong predation pressure, effectively homogenizing food webs in small streams. In the food webs I examined, predator-heavy food-web structures were apparently unable to persist in small habitats (unless subsidised by additional prey resources), so the pattern observed could be a "ghost of instability past" because food webs in small habitats are likely to be more easily perturbed (e.g., by disturbance or invasive species) than larger habitats. Although unsubsidised food webs did not support inverted biomass pyramids in small habitats, this does not imply that inverted biomass pyramids are unstable food-web structures. What it indicates, is that the stability of particular food-web structures is likely to change with habitat size, such that food-web structures that are stable in large habitats may not be stable in small habitats. Spatial coupling of prey by predators is likely to be one mechanism for why this change in

food-web stability occurs with a change in habitat size, and below I highlight several other possible mechanisms that might also explain this relationship.

Species richness (diversity) and evenness are often connected with food-web stability. For example, empirical evidence from long-term field experiments in grasslands suggest diversity and stability are positively correlated (Tilman et al. 2006). In both grassland and forested streams, species richness and evenness increased significantly with habitat size. Increased predator diversity can reduce the mean interaction strength of food-web links (Finke & Denno 2004), so an increase in predator species richness (relative to prey species) in streams may promote food-web stability through enhanced food-web complexity and an increase in weak interactions (i.e., greater food-web redundancy) (McCann et al. 1998). Thus, the stabilising effects of increased predator diversity may be one explanation for the increased stability of inverted biomass pyramids in larger habitats. In conjunction with an increase in species diversity with habitat size, there was also a decrease in predatory species dominance. A reduction in species dominance should result in interaction strength weakening as predator diversity increases via the same mechanisms as outlined above, although far fewer food-web studies have examined the effects of predator evenness compared with richness (Finke & Snyder 2010). Thus, there are very good reasons to link the more inverted biomass pyramids found in larger streams with food-web interactions that are made more stable by larger habitat size.

In addition to more general biodiversity–habitat size relationships, there are also likely to be system-specific mechanisms that mean food-web stability increases with habitat size. For example, in grassland streams, predator body size increases with habitat size. Large mobile predators are likely to ameliorate food-web instability by switching between prey species as their abundance varies because this provides predatory fishes with a more stable prey resource base and reduces predation pressure on prey populations when it is most needed

(i.e., when prey densities are low) (McCann et al. 2005). Switching to preying on terrestrial invertebrates when aquatic prey abundance is low may also reduce food-web instability in forested streams. Moreover, the stabilising effect of prey switching behaviour should be even more pronounced in forested streams because the high quality (i.e., low C:N ratio) of terrestrial prey items means that fewer aquatic prey may need to be consumed by predatory fishes (Edwards & Huryn 1996). Thus, both general and system-specific mechanisms may operate to maintain food-web structure and stability across habitats of different sizes.

Implications for food-web management in aquatic systems

Human activities (e.g., fishing) have a long history of targeting the top of food webs (e.g., Pauly et al. 1998, Jackson et al. 2001) and whilst the ecological consequences of large-scale predator loss in food webs are not well understood, we do know that once predator populations collapse, they may not recover (e.g., North Atlantic cod, Myers et al. 1997). Predator populations are stringently managed in many countries so they can be sustainably exploited (e.g., marine fishes, Yandle & Dewees 2008; freshwater fishes, Jellyman 2007), yet we do not appear to be managing the aquatic habitat of predators with the same effort. My research indicates that habitat size is a primary determinant of food-web structure, thus if managing a habitat or ecosystem to maximise predator biomass is a primary goal, this will be best assured by conserving large habitats. Cross-ecosystem subsidies can also dramatically increase the quantity of predator biomass a habitat can support, so for stream ecosystems, maintaining riparian-aquatic linkages should enhance a habitat's capacity to support predator biomass.

A change in a habitat's capacity to support predator biomass (and thus produce inverted biomass pyramids) may reflect not only the size of a habitat, but also its quality (e.g., whether it is impacted by human activities). Historical, pristine food webs in marine

ecosystems are very different from current ones (Jackson et al. 2001), and recent comparisons of coral reef fish assemblages in pristine and impacted habitats (i.e., fished by humans) have shown that top predators have been lost from these systems due to their susceptibility to over-exploitation (De Martini et al. 2008, Sandin et al. 2008). Furthermore, these studies conclude that the lack of inverted biomass pyramids currently observed in reef fish communities is indicative of the impacted condition of reefs globally. My research was conducted in relatively unimpacted stream habitats and found that inverted biomass pyramids were a relatively common feature. Such findings could be used in impact assessment by applying an observed versus reference condition approach. If streams did not support the expected amount of predator biomass for a given habitat size, it would be indicative of a decline in habitat quality and may suggest anthropogenic impact.

To understand variation in stream food-web structure, and how a habitat's capacity to support predator biomass changes with habitat size, both predator and prey communities need to be quantified. This is not surprising as stream ecologists have often found that biotic interactions are a strong determinant of fish communities (e.g., Power et al. 1985, Power 1992a, Nyström et al. 2003). However, many models for predicting changes in fish abundance (e.g., IFIM) still incorporate no assessment of prey availability, relying instead on physical habitat measures to predict stream community responses. My results indicate that to understand how predatory fish biomass will be affected by a change in habitat size, prey biomass must be quantified, thus seriously questioning the validity of predictive stream tools that do not estimate variation in prey abundance. However, my research highlights a new relationship that should advance our understanding of what causes variation in food-web structure which may also serve as the foundation of new analysis tools.

Plate 9. A rainbow trout (*Oncorhynchus mykiss*) from a stable spring (Photo credit: Angus McIntosh).

Chapter Six

General discussion: disentangling the drivers of stream food-web structure

Drivers of food-web structure in streams

Food webs are the result of organisms interacting with each other and the environment, yet predicting how they vary across environmental gradients is one of the greatest challenges facing ecologists (Chase 2005). Food webs are the product of multiple interacting drivers acting at several ecological scales (Hilborn & Stearns 1992, Lawton 1999), but my results highlight the importance of two ultimate drivers, natural environmental disturbance and habitat size, in determining stream food web structure (Fig. 1). These results contrast with existing models of aquatic community structure in which biotic interactions and physical processes have been viewed as competing forces (e.g., Peckarsky 1983, Menge & Sutherland 1987). Thus, my results suggest such a dichotomy may be misleading because disturbance and habitat size provide physical gradients across which biotic interaction strength and community responses vary. The best way to quantify or model food-web structure is still being debated (e.g., Allesina et al. 2008), but I have evaluated food-web structure based on the composition, biomass and size of predators and their prey, since food webs are basically a description of who eats whom in an ecosystem. My results illustrate how disturbance and habitat size affect a variety of community attributes, and in combination, the relationships examined in each chapter enhance understanding of key influences on food-web structure (Fig. 1).

Natural environmental disturbances (e.g., floods) can have strong effects on multiple trophic levels, although research has tended to focus on the lower ones (Wootton 1998). By focusing on stream fish, I have shown how disturbance influences communities through effects on both predator and prey biomass (Chapters 2 – 5), predator composition (Chapter 3),

and predator body size (Chapter 4). Most disturbance effects on food-web structure were via indirect pathways (e.g., disturbance → community biomass → food-web structure) (see Fig. 1), whereas habitat size directly influenced food-web structure but did not affect other attributes such as community biomass or composition (Chapter 5, Fig. 1). As disturbance and habitat size were not correlated in any of my studies, they had largely independent effects (although they had an interactive effect on predator body size). Only through quantifying the effects of both drivers on communities, could variation in food-web structure be fully understood in the streams I studied. Below I summarise how these findings contribute to a more comprehensive understanding of disturbance and habitat size effects in stream ecosystems, and how this new knowledge can advance conservation management and ecological theory generally.

A comprehensive understanding of the role of disturbance in stream food webs

Advancing a "disturbance framework" for stream ecosystems

Disturbance events are scale-dependent and hierarchical in nature (Frissell et al. 1986), because a disturbance at one level of ecological organisation may not be a disturbance at another (e.g., a small flood may remove particular invertebrate species but bring about no significant prey reduction or mortality to fishes). Given the diversity of biota and stream types, and the various scales at which freshwater ecosystems are studied, some researchers have suggested it is unlikely that one disturbance framework or metric will serve all needs (Stanley et al. 2010). Three distinct types of disturbance have been identified in streams: (1) pulse – short-term, and clearly delineated disturbance events e.g., floods; (2) press – a disturbance that may arise sharply and be maintained, e.g., dam effects or continual pollution;

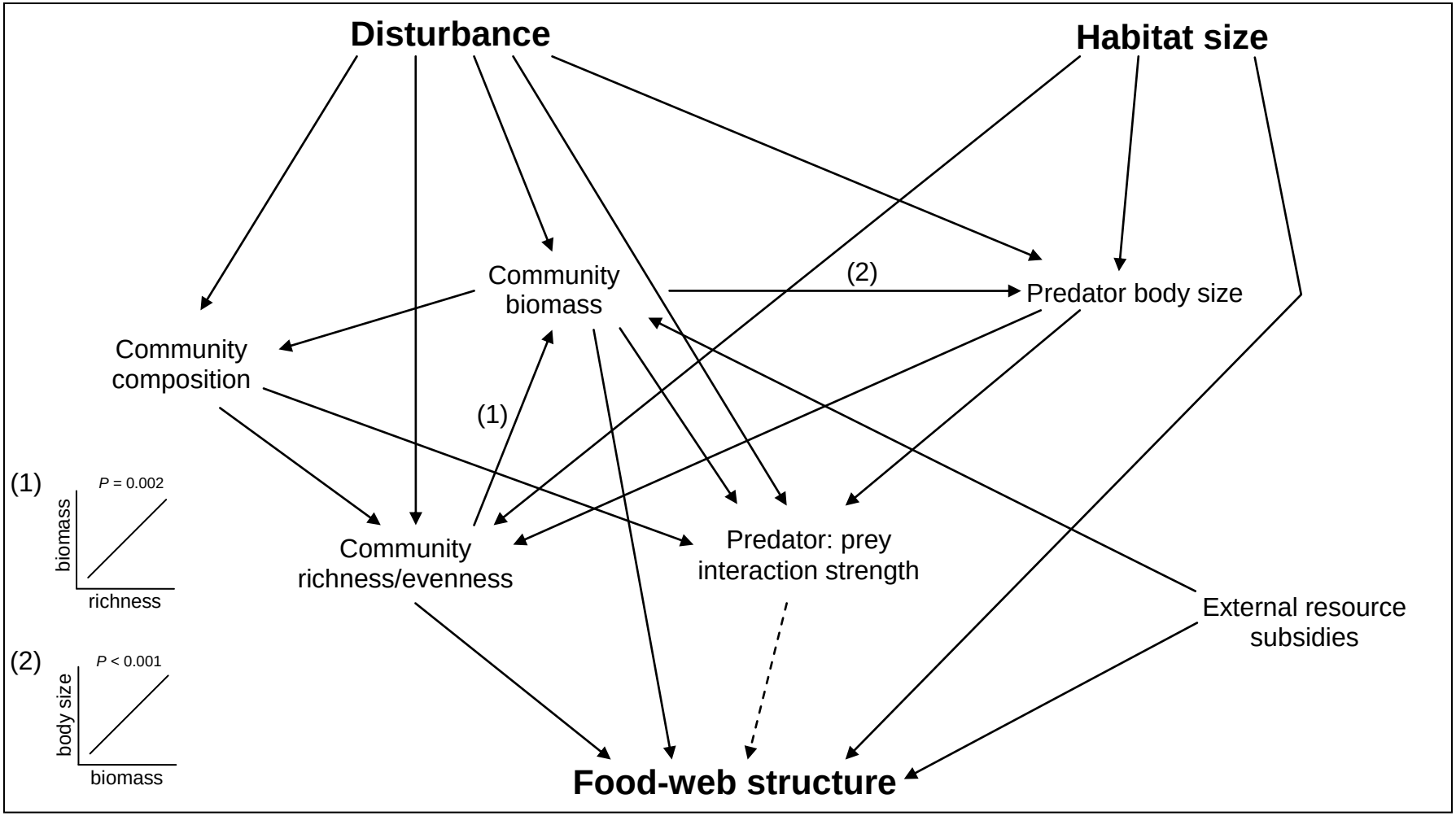


Figure 1. A synthesis of how disturbance and habitat size ultimately influence food-web structure (i.e., the amount of predator biomass relative to prey biomass) through a variety of pathways involving community composition, biomass and richness/evenness, body size and predator: prey interaction strength. In all instances, 'community' refers to both invertebrate and fish populations. Graphs one (1) and two (2) were constructed using data from 74 study sites (Chapter 4) to show the relationships/linkages between variables that have not been described in previous chapters. The dashed arrow represents a linkage that has been shown both theoretically and empirically to be important, but which was not directly examined in my thesis research.

and (3) ramp – a disturbance event that increases in strength over time e.g., droughts (see Lake 2000). Given this disturbance framework, a single metric that can quantify disturbance across all three disturbance types seems unlikely. Nevertheless, devising a standardised framework for disturbance studies within each disturbance type, and then comparing how increasing disturbance affects the severity of biotic impacts is likely to expand understanding of disturbance-related effects on stream communities. Beyond just identifying disturbance impacts on biota, such a framework should also facilitate a better understanding of complex disturbance effects, e.g., how disturbances to lower trophic levels can influence the abundance or composition of organisms at higher trophic levels.

My research focussed on flood (i.e., pulse) disturbances, because globally, floods are common types of natural hydrological events that remove many organisms from space. Thus, my conclusions are most applicable, but are not limited, to this disturbance type. Food webs are highly connected, and what influences one trophic level is likely to have direct or indirect effects on other levels. Therefore, at the scale of communities and food webs, it should be possible to utilise a consistent disturbance framework. I was able to use the same bed-movement related disturbance metric in all my studies (chapters) (i.e., river disturbance index, RDI), and this metric was highly correlated with many other disturbance measures and relevant to the fish studied (Chapter 2). In agreement with other studies examining disturbance effects on algal and invertebrate communities in New Zealand (e.g., Death & Winterbourn 1994, Clausen & Biggs 1997, Townsend et al. 1997b), I found bed movement was the strongest predictor of variability in stream fish assemblages. Increasing bed movement also directly reduced algal and invertebrate abundance, and indirectly decreased fish abundance. As these trophic levels are all responding to variation in bed disturbance, a framework where stream community structure is the product of bed disturbance mediated by flow variability is appropriate. The steep and gravel-dominated geomorphology of New

Zealand streams may increase the importance of bed movement relative to other aspects of disturbance that are more prevalent elsewhere (e.g., scour by entrained sediment) (Winterbourn et al. 1981). Nevertheless, because stream invertebrates are intimately associated with the stream bed, and fishes rely on invertebrates for food, stream communities should still respond more directly to bed movement than to flow variability. Moreover, since the relationships between flow and bed movement are complex (Biggs et al. 2005) it makes sense that bed movement-related disturbance measures are highly relevant to stream biota.

Quantifying how disturbance structures stream food webs

Using path analysis, I showed in Chapter 2 that the biomass of fish communities was influenced directly and indirectly (i.e., via invertebrate abundance) by disturbance, and that invertebrate communities were directly affected by disturbance (although invertebrate communities are probably also indirectly affected by reductions in algal abundance). To assess whether the observed disturbance-mediated biotic interactions affected the emergent properties of food webs in the streams studied, I conducted a further path analysis using quantitative biomass data from 65 streams in Canterbury and Westland, New Zealand (see Fig. 2). I examined whether the patterns in food-web structure supported my experimental evidence for strong biotic coupling between disturbance-induced variations in the abundance of unprotected or protected consumers (i.e., invertebrates that have/have not invested energy in a protective case/shell) and changes in predatory fish assemblages (Chapter 3).

As expected, this new path analysis showed a strong direct negative effect of disturbance on both protected and unprotected consumers (Fig. 2). Protected consumer abundance had a strong positive effect on eel biomass, but there was no evidence for a significant effect of protected consumers on either trout or galaxiid biomass. This was consistent with results from the *in situ* experiment where eel weight increased as the

proportion of protected consumer biomass increased (Chapter 3). Galaxiid weight did not significantly change with prey community composition in this experiment, but trout weight increased as the proportion of protected consumer biomass declined (Chapter 3). Unprotected consumers had a positive effect on trout and galaxiid biomass in the path analysis, indicating that both types of fish assemblage should be enhanced by increased abundance of unprotected consumers. Trout abundance had a strong positive link to the biomass of unprotected consumers in both mesocosm and *in situ* experiments (Chapter 3), and the significant connection identified in this analysis supported those results. Galaxiid biomass by comparison, was not significantly related to changes in prey communities in either mesocosm or *in situ* experiments, although a significant positive coupling between unprotected consumers and galaxiid biomass was identified in the path analysis. These results may appear contradictory, but they actually reflect the 'relict distribution' of galaxiid populations within stream catchments, rather than the galaxiid prey preferences that were tested experimentally. Galaxiids are often restricted to highly disturbed habitats because competition with trout and eels has resulted in their exclusion from stable and intermediately disturbed waterways (the habitats in which protected consumers are found) (see Woodford & McIntosh 2011). Unprotected consumers tend to dominate the prey community in disturbed habitats (Scrimgeour et al. 1988), so although galaxiids had no strong prey preference for unprotected consumers in the experiments (Chapter 3), they had a positive association with unprotected consumers in the path analysis due to their increased abundance in disturbed habitats. Even though galaxiid abundance was often low, they occur across the whole disturbance gradient (especially in trout-free refugia, McIntosh 2000a), and is probably the reason why no direct relationship was found between disturbance and galaxiid abundance. The path analysis showed that of the three fish groups, only eels were affected both directly and indirectly

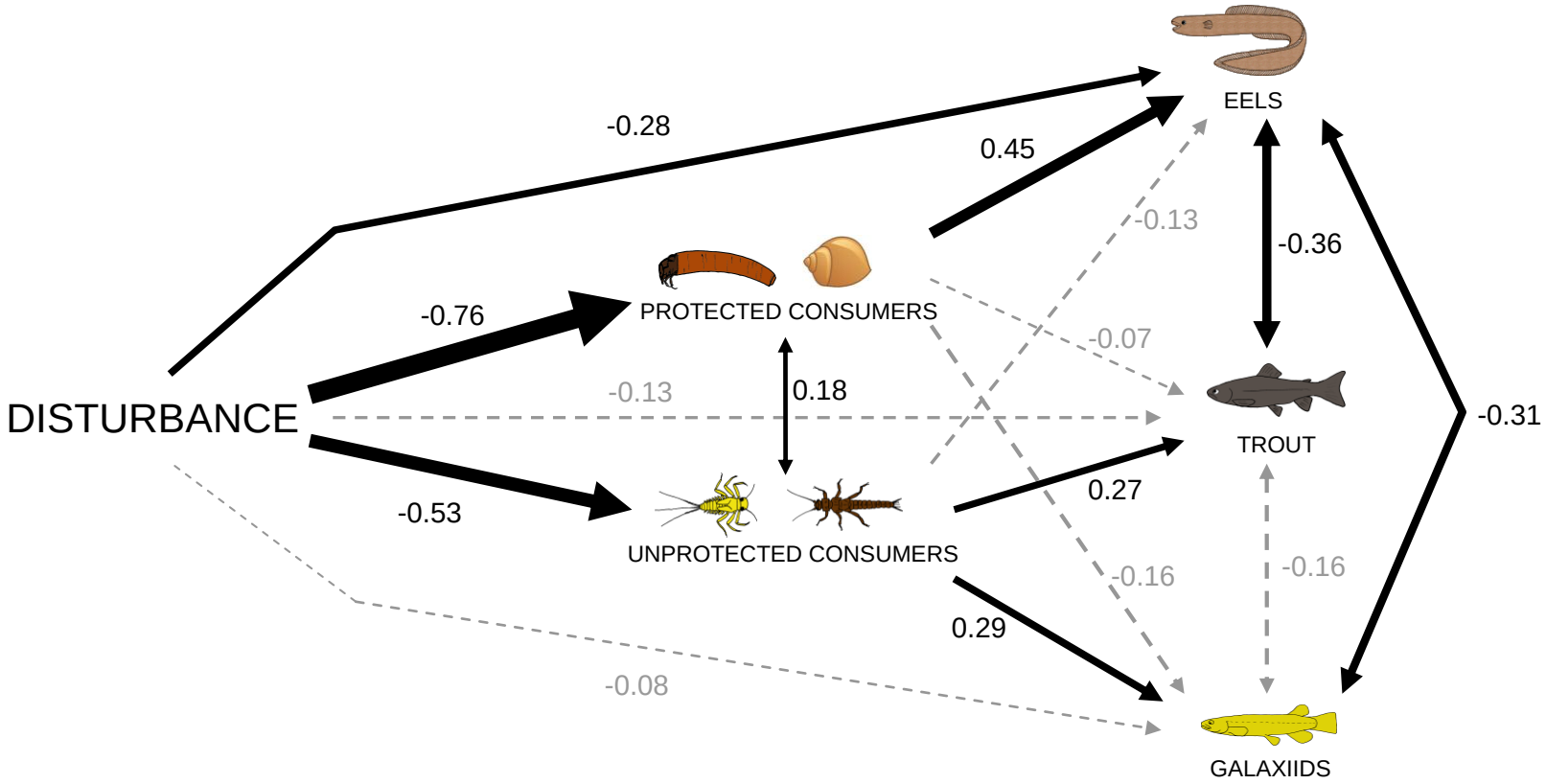


Figure 2. Path analysis of relationships between disturbance, consumer biomass and fish biomass for 65 grassland and forested streams in Canterbury and Westland, New Zealand. The path analysis was done on all sites for which I had consumer biomass (AFDM·m^{-2}) and fish species biomass (wet weight·m^{-2}), except sites that contained kokopu species (banded, shortjaw and giant) as these large, coastal dwelling galaxiid fishes are much different from the majority of galaxiid populations that were sampled during this study. As the model is over-parameterised, I set alpha at 0.1 so potentially important pathways were not ignored (due to Type II statistical errors). Dashed arrows indicate paths with $P > 0.10$, and solid arrows indicate paths with $P < 0.10$. The width of all arrows corresponds directly to their standardised path weights (for a further explanation of path analysis, see Data analysis section, Chapter 2).

(i.e., through prey) by disturbance. Eel biomass strongly declines with increasing disturbance (i.e., decreasing habitat stability), but the abundance of their major prey source, protected consumers, also strongly declines with disturbance resulting in a strong indirect effect of disturbance on eels.

These path analysis results summarise the relationships established in my surveys and experiments (Chapter 3), and show that disturbance-mediated shifts in prey communities result in fish community changes. The path analysis assessed the community data across the whole disturbance gradient, but disturbance-mediated food webs may be easier to comprehend when separated into three distinct disturbance categories (i.e., low, intermediate and high disturbance). Therefore, I used survey results identifying fish disturbance niches and changes in community biomass, as well as the experimental and path analysis results, to construct simple interaction webs for each disturbance category. These interaction webs were then combined with trophic position data from McHugh et al. (2010) to illustrate how disturbance-induced changes in prey communities likely affected food webs and food-chain length for each disturbance category (Fig. 3). Below I explain how these biotic interactions influence food-chain length in grassland food webs for each disturbance category, and why particular fish species/predator traits are likely to dominate under certain conditions.

In low disturbance habitats (i.e., RDI < 80), eels attain very large body size (Chapter 4), and because of this are able to consume all other fish and invertebrate species within the food web. They therefore attain a very high trophic position (Fig. 3). Niche overlap between eels and trout is substantial in stable habitats, but because the two fish types exploit different prey resources (Chapter 2, Fig. 2), interspecific competition for prey is probably low as Cadwallader (1975) suggested. However, this resource partitioning (i.e., eels consuming protected consumers and trout consuming unprotected consumers) likely explains why the impacts of predatory fish on prey communities can be high in stable habitats (Chapter 3). The

influence of intraguild predation on trout by eels is largely unknown (although trout up to 170 mm have been found in the stomachs of stream-dwelling eels in Canterbury, Cadwallader 1976), but as both species are known to prey on galaxiid fishes (Cadwallader 1976, McIntosh 2000a), eels must also be consuming some trout so as to attain a higher trophic position. Eel predation on trout was established in an early experimental examination of interactions between the two in Canterbury (Burnet 1968).

The abundance of protected consumers decreases significantly in intermediately disturbed streams (RDI: 80 – 110), the increase in disturbance having significant direct and indirect (i.e., via a reduction in protected consumer biomass) effects on eel biomass (Fig. 2). The body size of eels is significantly reduced in intermediately disturbed habitats (mean top predator size: low disturbance = 546 g, intermediate disturbance = 69 g; data from Chapter 4) and consequently, there is a large decrease in eel trophic position (Fig. 3). In contrast, the trophic position of trout is almost unaltered because their diets are largely unchanged. Trout still primarily consume unprotected consumers, but are likely to maintain a higher trophic position than eels by preying on galaxiids and predatory invertebrates (e.g., I observed over 50 *Archichauliodes diversus* larvae in one trout stomach!). There is a significant negative relationship between eel and trout abundance (Fig. 2), but the shifts in prey community structure between low and intermediately disturbed habitats mean that trout dominate intermediately disturbed streams, and can achieve high biomass.

Protected consumers are virtually absent from highly disturbed streams (RDI > 110), and consequently, so are eels. Trout also struggle to tolerate highly disturbed conditions because the availability of unprotected prey is low (Chapter 3). These conditions are also not conducive to predatory invertebrate species (e.g., *Stenoperla* spp., *Archichauliodes diversus*), because they have long life-cycles (Scarsbrook 2000), which are difficult to complete if regular disturbance events are occurring. Moreover, even though these prey communities are

almost exclusively composed of unprotected prey (which predatory invertebrates strongly prefer to consume, Devonport & Winterbourn 1976), prey supplies for predatory invertebrates were very low. This essentially results in a highly simplified food web where the only major biotic interaction is between galaxiids and unprotected consumers (Fig. 3). However, high disturbance does provide galaxiids with a relatively predator-free niche (McIntosh 2000a) although they can only attain low biomass because of the meagre prey resources available.

The effect of disturbance on predator-prey interaction strength

In freshwater habitats, investigations of biotic interactions have often been conducted under stable conditions (Power 1990, Gilliam et al. 1993), and whilst past research has provided important insights into the role of biotic processes, my studies indicate that biotic interactions vary in strength across the disturbance gradient. Hence, they are not necessarily strongest in stable habitats as previous research/models would suggest (e.g., Peckarsky 1983, Menge & Sutherland 1987). In stable habitats, prey organisms often invest energy in morphological defences (e.g., build protective cases) to reduce their vulnerability to predation (Wootton et al. 1996). I showed experimentally that the impacts of predatory fish on protected prey were consistently lower than on unprotected prey across the disturbance gradient. However, because protected prey are most abundant in stable habitats, and are at lower risk of predation than unprotected taxa, biotic interaction strength may not actually be highest in stable streams as predicted. Furthermore, interaction strength can also vary with the composition of the predator assemblage because predatory fishes differ in their ability to exploit particular prey taxa (Stallings 2010). Prey communities of intermediately disturbed streams are largely composed of unprotected taxa that drift more readily than protected prey and are at greater risk of fish predation (Chapter 3). Drift-feeding fishes (e.g., trout) are able to exploit these prey traits and exert strong predation pressure on unprotected prey communities (e.g., Huryn

1996, 1998), so the strongest biotic interactions may actually occur in these intermediately disturbed streams. Furthermore, intermediately disturbed streams contain simplified food webs (relative to stable habitats, Townsend et al. 1998), which have higher mean interaction strengths because they have fewer total interactions (i.e., reduced connectance), enhancing the strength of any single, dominant interaction (e.g., trout–unprotected prey, Fig. 3). In combination, these factors indicate that disturbance and prey community composition should strongly influence predator assemblages and the strength of predator-prey interactions. My results also suggest that models of community structure, which assume that biotic interaction strength weakens with increasing disturbance, may be overly simplistic. This is because changes in interaction strength are likely to be strongly associated with the traits of both the prey and predator communities, as well as the abiotic context in which the interactions occur. Thus, the results of my disturbance studies highlight the importance of recognising how the strength and outcome of species interactions can vary as a function of biotic and abiotic context.

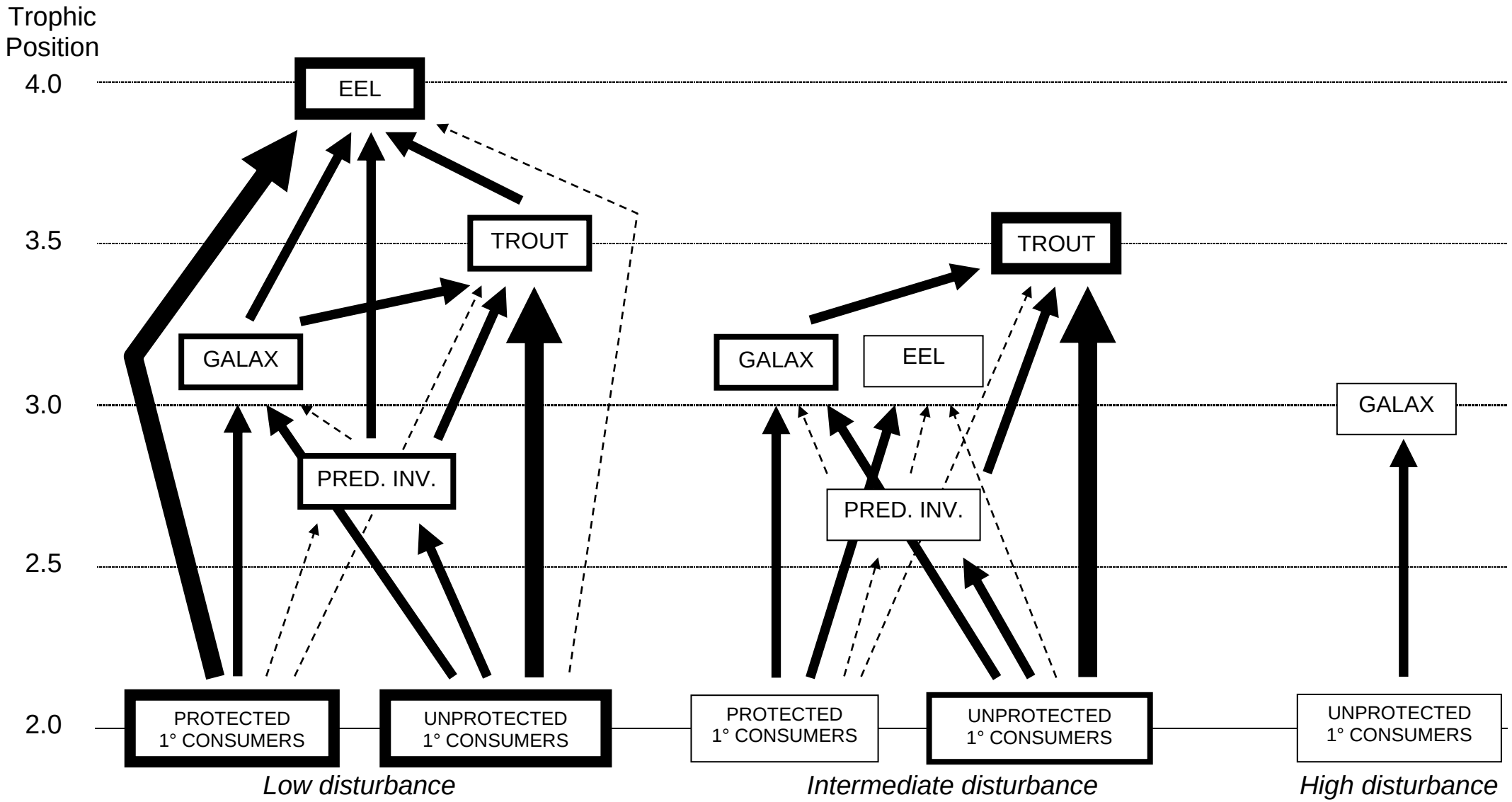


Figure 3. Hypothesized interaction webs showing how the trophic position of various groups changes in three kinds of disturbance-mediated prey assemblages. The thickness of each box outline shows how the biomass of each group changes at the three disturbance levels. Wide solid arrows convey a large biomass transfer between linkages, thin solid arrows a moderate transfer and dashed arrows a small transfer. The piscivorous interactions shown have been documented by Cadwallader (1975) and McIntosh (2000a). Eels greater than 25 cm long (the minimum eel size in these streams) are not eaten by trout. The trophic positions of fishes and predatory invertebrates are from McHugh et al. (2010). GALAX = galaxiid, PRED. INV. = predatory invertebrates.

Using the results of my research to advance understanding of food-web structure

Disturbance and habitat size are recognised as critical determinants of food-chain length (Marks et al. 2000, Post et al. 2000, Thompson & Townsend 2005, McHugh et al. 2010), but my research has shown they also ultimately control stream food-web structure (Fig. 1). As previously discussed, determining how food webs respond to changes in these drivers is vital for predicting how ecological communities will be influenced by global change phenomena such as habitat contraction and altered disturbance regimes (IPCC 2001, Foley et al. 2005, Milly et al. 2005).

Food-web structure changed dramatically across the habitat size gradient provided by my streams (Chapter 5). The distribution of biomass in food webs became increasingly inverted as habitat size increased, and was highly predictable. Effectively, larger habitats supported a larger amount of predator biomass relative to prey biomass compared to smaller habitats. Increasingly complex food webs were also present in larger habitats (i.e., an increasing number of predatory species were being supported in larger habitats), a condition that has previously been associated with increased food-web stability (Finke & Denno 2004). In contrast, recent research by Neutel et al. (2007) showed that by keeping a relatively high proportion of biomass at the bottom of the food web (i.e., preserving a 'pyramidal' shape), soil food webs increased in complexity whilst maintaining their stability. My results show that increased complexity is associated with a high proportion of biomass at the top of the food web, not the base of the food web. Whether these divergent results are due to different mechanisms operating at contrasting scales, or arise because soil food webs are inherently different from stream food webs, remains to be seen. However, for stream ecosystems, the implications are clear: if stream habitats become smaller (e.g., through water abstraction) they will support less predator biomass, and if disturbance regimes are altered, food-web structure will be affected.

Is it time for a shift in conservation thinking for stream ecosystems?

Keeping sufficient water in streams and rivers so that natural disturbance regimes are retained and habitat size is not reduced is one of the major challenges encountered when trying to conserve stream ecosystems. This is partly because there is insufficient scientific knowledge as to how much water must be retained to conserve ecosystem processes and species, but it also highlights a lack of public awareness surrounding the importance of freshwater environments as well as the species they contain. Whilst the plight and decline of terrestrial species (e.g., native birds) often garners much public and funding support, a similar appreciation for indigenous freshwater taxa is yet to be attained (Allan & Flecker 1993, Baillie et al. 2004, McIntosh et al. 2010). For example, it would be difficult for most New Zealanders to name a native freshwater fish species that was in danger of extinction, yet the majority would know that kiwi and kakapo were highly vulnerable. Consequently, many terrestrial habitats in New Zealand have long been protected (e.g., Tongariro National Park was established in 1886) to ensure that iconic terrestrial landscapes and species are conserved. In contrast, the preservation of freshwater species has largely been inadvertent, with aquatic organisms only gaining (until recently) a level of protection if they inhabit waterways within a terrestrial conservation area. Many streams outside protected areas are exploited to varying degrees (e.g., water abstraction, hydro-electric generation, municipal uses), although high-value areas within a landscape may often get some level of protection if an endangered species is present. This conservation model has been implemented in many locations around the world but is now deemed to be inadequate for the preservation of stream ecosystems (Moyle & Randall 1998, Saunders et al. 2002) as it is thought to provide only a "weak safety net" for aquatic features and species (Herbert et al. 2010). With this in mind, it is poignant to ask: Is it time for a shift in conservation thinking for stream ecosystems?

In New Zealand, there has been a recent realisation that specifically conserving only terrestrial areas will be inadequate for the successful protection of freshwater ecosystems (Chadderton et al. 2004). Furthermore, there is increasing recognition of the importance of streams in maintaining ecosystem function and health, in addition to our global responsibility to maintain biodiversity; New Zealand's invertebrate and fish faunas have a high level of endemism (McDowall 1990, Winterbourn 2004). To assist in prioritising freshwater conservation efforts, research involving modelling the influence of landscape-scale factors on stream communities has been undertaken (Leathwick et al. 2008, 2010). There is a welcome and more general attempt to shift conservation in New Zealand towards an ecosystem management approach, whereby success is best assured by conserving and managing the ecosystem as a whole, rather than with an individual species focus (Christensen et al. 1996, Poiani et al. 2000). However, our ability to model changes in stream habitat types is far superior to our understanding of the ways in which stream communities respond to variations in environmental drivers (e.g., disturbance), so my research which has focussed on two drivers of stream food webs, has a number of implications for ecosystem-scale models and conservation management (e.g., how changes in habitat size and disturbance affect the abundance, body size and composition of stream fish communities).

Biodiversity is declining at a far greater rate in freshwater ecosystems than even the most affected terrestrial ecosystems (Ricciardi & Rasmussen 1999), and habitat-size reductions and fragmentation of habitat due to dams and water abstraction are amongst the major contributors. Such actions result in streams/rivers with altered disturbance regimes and reduced habitat size, which have major effects on lotic communities as my research has shown. A reduction in habitat size has two major effects on stream communities, the first of which is that top predator body size decreases (Chapter 4). The loss of large predators from a community has important theoretical implications for food-web stability (McCann et al.

2005), but it also has well established effects on fish populations. The largest fishes within a community are the most fecund and produce the largest number of eggs to sustain future populations. Therefore, maintaining large fishes is a priority for both commercial (e.g., eel) and recreational fisheries (e.g., whitebait, salmonid) in New Zealand. In addition to predator body size, a reduction in habitat size is also likely to affect the ability of a food web to sustain predator biomass (Chapter 5). My research showed that food webs did not support a constant amount of predator biomass across the habitat-size gradient; large habitats actually supported disproportionately more fish biomass and greater fish species richness than small habitats (Chapter 5). From an ecosystem management perspective, these results indicate that if more water can be kept in a river, thereby enhancing the presence of large habitat, then larger, more diverse fish communities will be present.

It has been predicted that stream ecosystems will be strongly impacted by global climate warming, because runoff patterns, base-flow discharge and the frequency and magnitude of extreme events are all likely to alter (IPCC 2001, Milly et al. 2005). In New Zealand, predictions suggest that annual and seasonal rainfall will be reduced but that daily rainfall and hence flood magnitudes will be increased (McMillan et al. 2010). My research has shown that disturbance has important effects on stream communities (Figs. 1-3), so a predicted increase in stream disturbance can be expected to have important consequences. An increase in the number and size of flow-related disturbance events should decrease predator size, although changes in body size are likely to be influenced more by the effect of climate warming on habitat size than on disturbance (see 3-d graph Chapter 4). Thus, minimizing disturbance events through flow capture/diversion is not a realistic solution because of the direct effect it will have on reducing downstream habitat size. In New Zealand, for example, an increase in disturbance will have negative impacts on both protected consumers and the eel populations, which are strongly linked to them. In turn, this may result in a greater proportion

or biomass of unprotected prey, which could benefit trout, allowing them to invade habitats dominated by eels. However, an expansion in the distribution of trout may be partially offset by their being excluded from disturbed waterways, which can no longer support their energetic requirements. Likewise, an increase in summer temperature may decrease disturbance and have the opposite effect on fish community structure (e.g., increase eel abundance due to more stable habitat conditions). More stable habitats should result in an increase in the abundance of protected consumers, and have important consequences for fish communities (e.g., an increase in eel biomass). Higher mean summer temperatures may also increase the frequency and duration of droughts, with probable declines in discharge, habitat size and invertebrate community size. However, our ability to predict exactly how droughts may affect community structure is limited at present (Lake 2000).

Whilst our understanding of ecological impacts associated with droughts is limited, I suggest it is far superior to our knowledge of the ways that cross-ecosystem linkages can influence community structure. An ecosystem-orientated management approach recognises that stream food-web interactions can be complex, because far from being isolated habitats, important food-web interactions often occur between streams and their adjacent habitats (e.g., freshwater and terrestrial environments; Nakano & Murakami 2001, Baxter et al. 2005). A reciprocal exchange of prey subsidies between habitats can support increased predator populations (e.g., fishes and birds) in both habitats (Nakano & Murakami 2001), and my research showed that terrestrial prey subsidies such as insects can support increased fish communities across a range of stream sizes, not just small headwater streams (Chapter 5). Research investigating cross-ecosystem linkages has been steadily increasing over the last ten to fifteen years, during which ecologists have developed a more holistic understanding of what influences food webs (e.g., Polis et al. 1997, Greenwood & McIntosh 2008). A consequence of this increase in knowledge and understanding is that conservators and

managers of stream ecosystems need to incorporate a recognition of landscape influences on food-web structure into their programmes. An ecosystem management approach enables such a framework to be built (whereas species-specific strategies do not), as it can incorporate concepts such as biotic interactions and cross-ecosystem linkages, whilst also recognising that activities which have an impact on one ecosystem (e.g., agriculture and forestry practices in terrestrial habitats) can also have significant effects on the species and structure of food webs in recipient ecosystems (e.g., streams, lakes, estuaries and oceans).

Conclusion

As humans intensify land-use activities, fragment habitats, over-exploit species and 'warm up' ecosystems, they have a major impact on ecological communities (Didham et al. 2007, Banavar & Maritan 2009). Major outcomes of these human actions include alterations to natural disturbance regimes and changes in habitat size. The results of my thesis research indicate that to predict how these changes will affect food-web structure, ecologists will need to consider the separate and interactive effects of them on a variety of food-web attributes (Fig. 1). Because changes in the strength of these drivers can alter community biomass, composition, body size etc. (Fig. 1), it is essential that we understand how the various food-web attributes fit together and interact so we can predict how food-web structure is likely to respond to future variation in these drivers. As many ecosystems are changing at an unprecedented rate (Banavar & Maritan 2009), conservation management must be adaptable so that scientific advances can be quickly integrated into its operating framework. My research suggests that as we move towards an adaptive ecosystem-management framework, disturbance and habitat size need to be recognised as the key drivers of stream food webs if the effectiveness of conservation measures is to be improved.

Acknowledgements

Ahhh…the day to write acknowledgements has finally arrived, so the finish line is in sight! The fact that I am actually seeing a finish line means that I have many people to thank for getting me this far. Firstly, to my primary supervisor Angus McIntosh, for whom an 'acknowledgement' will never cover all that he has done for me over the years. As a 2nd year student I had never considered doing post-graduate study but that all changed when Angus arrived half-way through a freshwater summer field course and started teaching me about all things fishy (and later joining in our student soccer game didn't hurt his credibility with me either!). His enthusiasm, encouragement and knowledge inspired me then and have continued to do so in the years since. Thank you to my associate supervisors, Jason Tylianakis and Dave Arscott, for their support and expertise and for always being willing to discuss statistical problems or offer feedback on experiments and chapters. I also owe a big thanks to Pete McHugh, my unofficial fourth supervisor, who has always made time to advise me on statistical issues (thus preserving my sanity during fierce battles with R) and offer feedback on various versions of my chapters. Although he is departing shortly for a job in Portland, this will still not stop me pestering him for advice but I wish him and Katie all the best in their new jobs. Thanks to Jon Harding for all of his work in co-running the Freshwater Ecology Research Group, (FERG) and for always having an open door for a chat (and a laugh) about life and science. A massive thanks to Mike "The Godfather" Winterbourn for his prompt editing efforts that helped to get this thesis "over the line". Although retired, his continued passion for research and willingness to help all FERG students continues to amaze me. It has been a privilege to work in FERG for many years, and past and present members have all contributed to making university a fun and productive working environment.

In thanking my field assistants, a special acknowledgement must firstly go to those who endured the sub-zero temperatures of my dreaded mid-winter fish surveys. Memorable moments included…the original helper/victim/flatmate Brendan Coffey declaring on our first day of field work "I have never been this cold in my life!" unfortunately that was the same day I later uttered the infamous phrase "I'm pretty confident there'll only be a couple of fish at this site"…3 vs 300 fish…sometimes ecology is not an exact science! After years doing similar field work it was always great to have dad come up in the weekend to provide his

fishy wisdom…I think “harden up” was his favourite motivational catch phrase. I can clearly remember this morale-boosting advice used on multiple occasions when the feeling had long since left my hands after measuring rocks in 0.5 °C river water. And lastly to Christa (who racked up the most electrofishing hours of all), who on her first trip said “I don’t mind picking up these fish but I’m not touching those ones!” - I think it is safe to say that Christa’s love for eels never quite reached the levels of my father.

A number of other people have helped with experimental setup, field and laboratory work, and their time and effort is much appreciated. In particular, Darragh Woodford, Steven Lowe and Andrew Memory, who along with those people previously mentioned, put in a massive amount of work to get some of my “rather ambitious” field experiments up-and-running. Thanks also to Kristy Hogsden, Hamish Greig, Amanda Klemmer, Simon Howard, Troy Watson, Danladi Umar, Helen Warburton, Cherie Ross, Jo Ocock, Matthew Langley, Rachel Saunders, Alex Ross, Richard White and Christy Thomas.

A number of technical staff at UC have donated their expertise to make this project possible: Linda Morris for the help provided to me during my research and all that she does for FERG; Nick Etheridge for advice on equipment construction and any random related modifications, and also for our many chats about all things sports and fly fishing; Nikki Judson, Penny Moore, Lyn de Groot, Liz Fitzgerald, Nicole Lauren-Manuera and Selwyn Cox for their work in organising post-grad events and all things administrative; John Scott and Graeme Young for computer assistance. Thank you also to Katie McHugh for her patience and assistance when I was producing my various maps.

Alistar Suren and Paul Sagar at NIWA, Christchurch kindly allowed me to use field equipment and data (fish dry weights), respectively. My ‘ambitious’ fish cage experiment would not have been possible without the generosity of Alistar, who having invested so much of his own time in constructing the cages, allowed me to deploy them in the often unpredictable rivers around Cass. Thanks also to Dave West (Department of Conservation) for supplying community and physico-chemical data from Coromandel streams.

Thank you to the landowners from Porters Pass through to Bealey pub who have all granted me access to conduct my research for many years in the Canterbury high country. Particular thanks to Christine Fernyhough for being interested and agreeable to the strange request of two students to put fences down the middle of the streams on her property.

This research would not have been possible without a UC doctoral scholarship, funding from the Brian Mason Scientific and Technical Trust, and travel grants from NABS Petersen fund, the SIL travel trust fund and New Zealand Freshwater Sciences Society.

To my family, immediate and extended, thank you for your love and support (in too many ways to name) during my thesis. Lastly, I must again thank my fiancée Christa for her love, hard work and patience during my Ph. D (and apologise to her for ending my thesis with a fishing pun in her honour). There are not many partners out there who would spend their holidays stringing together shadecloth fences, carrying fish cages around the high country or trudging through thigh-deep snow to help out with mid-winter electrofishing surveys…I think I've bagged me a keeper!



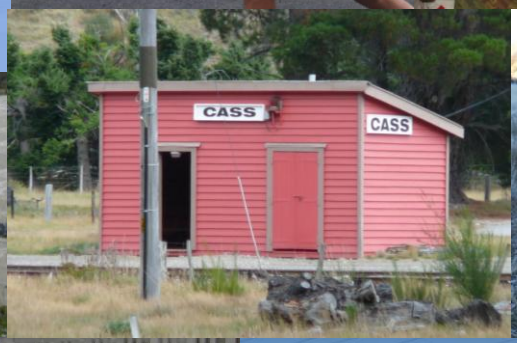




FERGBURGER



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